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DYNAMICS OF FERTILIZER AND NATIVE NITROGEN IN A DOUGLAS-FIR ECOSYSTEM

by

GEORGE E. NASON

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
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DEDICATION

To the memory of Mom and Dad

ABSTRACT

Nitrogen cycling in a 38-year-old, medium-productivity stand of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on a coarse-textured podzolic soil of southeast Vancouver Island, B.C. was examined after spring and fall application of N at 200 kg ha^{-1} as ammonium nitrate (AN) or ^{15}N-enriched urea.

Volatilization was equivalent to 14% of spring-applied urea-N but was negligible in other treatments. Amounts and ^{15}N abundance of volatilized N were a function of post-fertilization rainfall (2.4 and 94 mm in the first week after spring and fall fertilizations, respectively). Recovery of ^{15}N in Douglas-fir seedlings potted in peat above the urea plots demonstrated ammonia recapture by understory vegetation could occur.

Douglas-fir responded to N-fertilization by increasing: the N concentration of existing foliage and both the concentration and content of N in new shoots. At the first fall after fertilization (seasons of application combined), AN caused a 26% increment over control in N content of current foliage whereas urea gave a 13% increase. This superiority of AN over urea was attributed to the nitrate ion. The hypothesis that N uptake into foliage from AN would be greater when applied in spring was not supported.

Recovery of urea-N in soil was complete at 3 weeks but declined to 50 to 60% at 2 years. The balance of the fertilizer N was accounted for by Douglas-fir uptake and volatilization. Availability of N declined exponentially such that 6 months after fertilization only 5-10% of applied N remained in inorganic forms. Fifty percent of urea-N was immobilized within 3 weeks of application. Fertilizer uptake to foliage at one year was 15 and 21% of applied for the spring and fall applications, respectively. From kinetic analysis of tracer data in one-year-old foliage and soil ammonium fractions, the rate of uptake of N in the first year by fall-fertilized trees was about double that by spring-fertilized trees.

A simulation model utilizing two kinetic fractions of both foliar N (mobile, structural) and soil organic N (active, stabilized) accounted for most of the variation in the soil and foliar N and ^{15}N abundance data obtained in the first year after spring fertilization.

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1. INTRODUCTION

Temperate and boreal coniferous forests are limited in their growth by nitrogen more commonly than by any other nutrient element (Wollum and Davey 1975). Models have appeared recently that relate nitrogen nutrition to growth performance of conifers (Ingestad 1987, Ågren and Bosatta 1988). The central features of these models are: first, dry matter production is expressed as the relative growth rate and this is a function of total N in the canopy; second, N uptake is regulated by the soil N flux density, i.e. diffusion of N to roots is the rate limiting step. Hence, growth in a given year is a function of the accumulation of N over at least one, if not several, previous years. Consumption of N during growth draws down reserves, and ultimately ties growth to the availability of N in soil. Availability of N in soil is adjusted by addition of nitrogenous fertilizers.

Scandinavian foresters have fertilized coniferous forests with N for over three decades. Yet fertilized forest land in North America is about 10% of that in Scandinavia (Ballard 1984). One reason for slower implementation of fertilization in North America is lack of satisfactory response prediction. Advantages gained in treatment of responsive stands may be offset by losses in non-responders. Thus, there is great interest in the fate of applied N and what practices might optimize this with respect to tree uptake.

Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) in coastal British Columbia and the U.S. Pacific Northwest is a species of great economic importance. This species is responsive to N but, only rarely, any other element. A regional response to N @ 224 kg ha^{-1} averages 18% in merchantable basal area over a 10 year period (Gessel 1984) and may result in a return on investment of as much as 30% (Fight and Dutrow 1981), but considerable variation occurs. Stand and site factors that contribute to this variation include stocking levels, site index (Heilman and Gessel 1963), S-status (Turner et al. 1977), forest floor C/N (Edmonds and Hsiang 1987) and age of trees (Miller et al. 1975). Treatment variables under control of a forest manager include rate, timing and chemical source of N applied.

Growth response to N fertilization is curvilinear with an upper limit set by toxicity, or limitations of resources such as water or photosynthetically-active radiation. Rates that maximize growth response per unit of applied N are typically in the range of 150-250 kg N ha^{-1}. Operational fertilization in Sweden is usually at a rate of 150 kg ha^{-1} (Malm and Möller 1975). In the Douglas-fir region application rates have tended to be somewhat higher.

Timing, as currently discussed, relates to the season in which fertilization takes place. Selecting a season for application involves simultaneous consideration of climatic and soil conditions (Ballard 1984), and the phenological condition of the target trees. From the research to date in Douglas-fir forests, sufficient information is available to rule out winter and summer as candidate seasons. The timing of uptake of nutrients by conifers is not well understood. It has been assumed that uptake potential is related to the abundance of new short roots and this, for Douglas-fir, would mean additions of available nutrients in spring to coincide with maximum uptake. Rainfall and temperature patterns, however, interact with soil and fertilizer sources to control available nutrient dynamics.

The common N fertilizer sources used in forest application are urea ($(NH_2)_2CO$) and ammonium nitrate (NH_4NO_3, abbreviated AN). The higher N content of urea (46 vs 34%) reduces the total mass to be handled - an important consideration, and potential advantage, because fertilizers are generally applied by helicopter. In Scandinavia, however, response of Scots pine and Norway spruce to AN is typically 30% more than to urea greater over a 5 year period (Malm and Möller 1975). In the Southeast U.S. little difference has been found between the two sources (Fisher and Pritchett 1982). For Douglas-fir in British Columbia and the Pacific Northwest, Miller and Harrington (1979) and Miller et al. (1986) found no difference but data of Miller and Reukema (1974) and Dangerfield and Brix (1981) were consistent with the Scandinavian experience .

Volatilization and immobilization divert urea-N from trees. The first pathway is ephemeral, and results from the release of alkali accompanying the biological hydrolysis of urea. Losses of ammonia to the atmosphere can occur when the soil buffer capacity is saturated in localized zones (Overrein 1968). Temperature, soil moisture and wind speed affect the rate of volatilization (Watkins et al. 1972). The rate of the second pathway, immobilization, may increase after urea fertilization and prevent ammonium ion from reaching tree root systems and associated mycorrhizae (Johnson et al. 1980).

Process-level information needed to understand fertilizer responses is inadequate, often because only a part of the soil-plant system was studied. For example, the important factors regulating the rate of volatilization of ammonia from urea fertilizer have been identified with laboratory experiments but extent of the process has received little attention under field conditions. Further, the fate of volatilized N is rarely followed. Immobilization studies have most often been conducted in the laboratory with plant-free microcosms. Studies of stand-level N cycling in coniferous forests have involved ecosystems that are not representative of intermediate productivity stands. For example, concepts of conifer response to fertilization, which emerged largely from the work of H.G. Miller and colleagues in Scotland (Miller 1981, Miller et al. 1979, Miller et al. 1981) and H. Brix and colleagues in British Columbia (Brix 1981a, Brix 1981b, Brix 1983), are based on soils of low fertility. Other detailed studies of stand-level N cycling have, for practical reasons, been carried out in very young plantations.

The present work was undertaken to examine N cycling in a Douglas-fir stand typical of a high priority candidate for commercial fertilization. This involved identification of an intermediate productivity stand, near the peak of its annual N requirement, of sufficient size to accommodate a controlled experiment. Such a stand was located on the lands of MacMillan Bloedel Ltd. in the Northwest Bay Division, situated on east-central

Vancouver Island. The principal objectives were:

1. Examine in the field the role of temperature and precipitation in the regulation of volatilization after urea fertilization.
2. Test the hypothesis that volatilized N can be recaptured by plants.
3. Test the hypothesis that timing of application (spring vs. fall) and chemical source of N (urea vs. AN) are not determinants of N uptake by intermediate productivity Douglas-fir.
4. In urea-fertilized plots:
    a) quantify the fate of added N
    b) estimate rates of mineralization, immobilization and plant uptake
    c) simulate the state of soil and foliar N
5. Estimate growth response to N fertilizers and interpret results relative to N nutrition.

A completely randomized plot design was established and ^{15}N-Urea and AN in granular form were broadcast to plots in both spring and fall. Periodic sampling of volatilized ammonia, forest floor, mineral soil, and current and one-year-old foliage of Douglas-fir was performed. Rates of N cycling processes in urea treatments were estimated from kinetic analysis of the ^{15}N data. Concepts that were useful in explaining the functioning of the fertilized ecosystem are organized in a computer simulation model presented in the last chapter.

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2. SITE DESCRIPTION AND EXPERIMENTAL DESIGN

2.1 Study Site

The study site was located approximately 14 km NW of Nanaimo on the east side of Vancouver Island (49° 15' N lat., 124° 10' W long.) at 300 m elevation (Fig. 2-1) and is within the Wetter Coastal Douglas-fir Biogeoclimatic Subzone of Klinka et al. (1979). The climate in the area is characterized by cool wet winters and warm summers that usually include a droughty period extending from mid-July until October. Snow seldom persists for more than two weeks. Annual precipitation varies from 90 to 140 cm; the majority falls as rain during late fall, winter and early spring.

Extensive glaciation has occurred but local materials are dominantly porphyritic basalts and surficial materials are characteristically coarse. Topography in the area is bedrock-controlled, highly dissected, and slopes range to 20%. The study site is located on a bench where slopes are less than 5%. The soils are rapidly drained and have formed from a relatively thin (75 to 125 cm thick) gravelly, loamy sand till overlying basaltic bedrock. They are classified as Sombric Humo-ferric Podzols (Agriculture Canada Expert Committee on Soil Survey, 1987) or Haplorthods (Soil Survey Staff 1975). A description of a typical profile is presented in Table 2-1.

Soil Characterization

Textural, X-ray diffraction, and cation exchange capacity (pH 7, 1M NH_4OAc) analyses followed methods in McKeague (1978). The fine earth fraction of a bulk 0-15 cm sample was 84% sand and 2.8% clay, the majority of which was chlorite and kaolinite. Thus, most of the cation exchange capacity, which varied from 32 in the Ahe to 12 cmol(+) kg^{-1} in the BC2, was supplied by organic matter. Organic matter accumulations were considerable (Chapter 3) and were especially prominent in A horizons containing high proportions of cobbly coarse fragments. The C/N ratio was remarkably wide (Chapter 3)

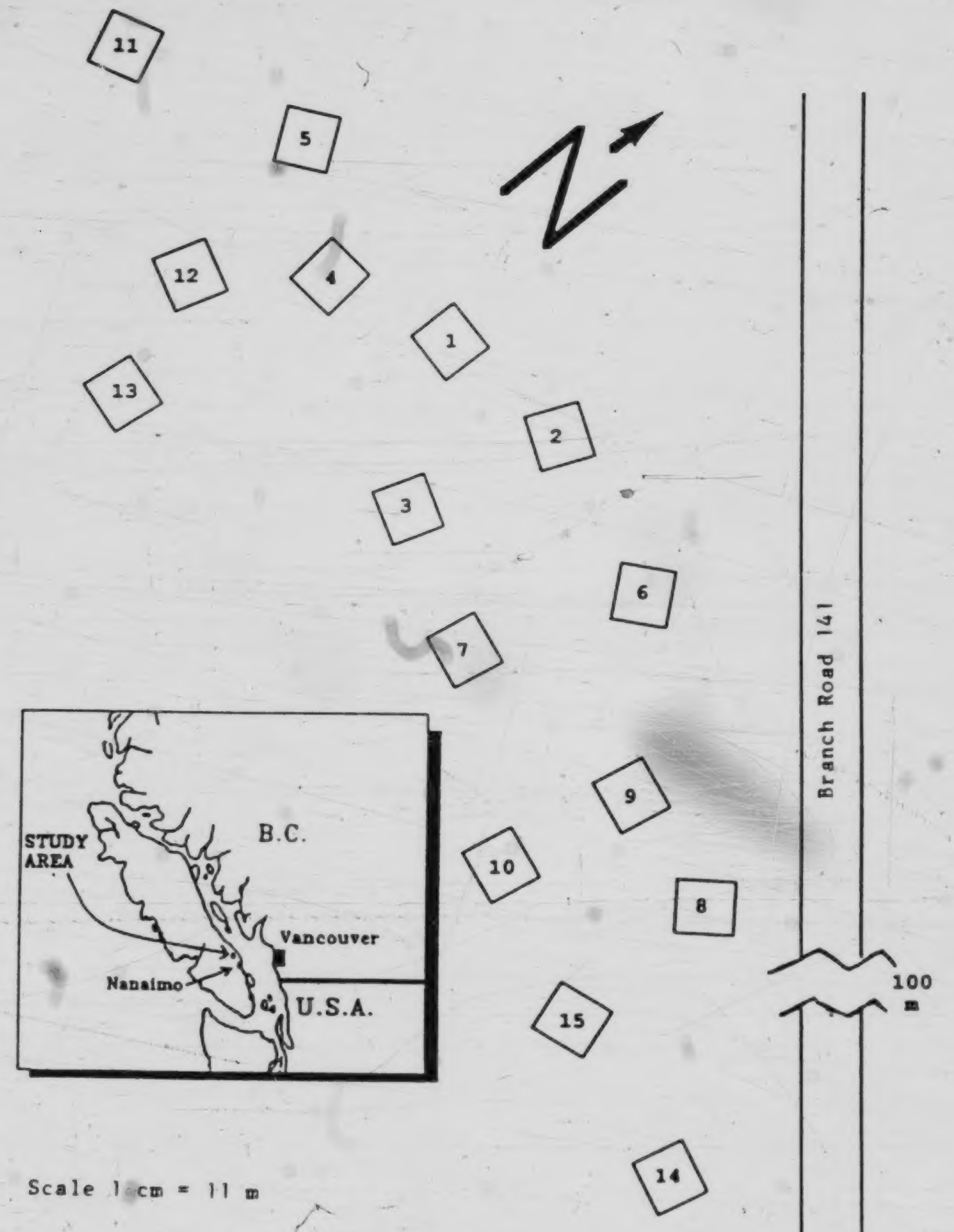
11
5
N
12
4
1
13
2
3
6
7
Branch Road 141
9
STUDY AREA
B.C.
10
8
Vancouver
Nanaimo
U.S.A.
100 m
15
14
Scale 1 cm = 11 m

Figure 2-1. Location of study site and arrangement of plots. Plots were 11 X 11 m.

and decreased with depth within material type - organic or mineral. The forest floor consisted of discrete L, F and H horizons (Oi, Oe and Oa respectively in Soil Taxonomy). In the F and H horizons fungal mycelium was often extensively enmeshed with decomposing litter materials.

The modal humus form was mormoder (Klinka et al. 1981) but, over much of the site, had a thicker A horizon than defined for this subgroup and thus, intergraded to leptomoder. Substantial variation in the humus form occurred over short (<2 m) distances and appeared related to windthrow, localized restrictions in vertical drainage imposed by concavities in the bedrock, and perhaps vertical relations with canopy architecture (Crampton 1982). In particular, the depth of the Ahe horizon varied from over 15 cm depth in rocky and/or microdepressional areas and near tree boles, to being absent altogether in more open parts of the stand where throughfall could be expected to be greatest. In addition, coarse woody debris was estimated to comprise 5-10% by area of the forest floor. Such variation complicated classification but is normal in the region (Crampton 1982, Carter and Lowe 1986).

Vegetation

Vegetation consisted of a naturally regenerated 38-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) overstory of approximately 1000 stems ha^{-1} and a patchy, moderately dense (% cover varying from 20 to 55) understory dominated by salal (*Gaultheria shallon* Pursh) with minor components of Oregon grape (*Mahonia nervosa* (Pursh) Nutt.) and bracken fern (*Pteridium aquilinum* (L.) Kuhn). The site index (30 m at 50 yr) indicates intermediate productivity for this region.

Two meteorological stations were established within the stand. Soil temperature at 0 cm depth and both air temperature and relative humidity at 15 cm above the forest floor were continuously recorded using analog equipment. Throughfall was measured at three

Table 2-1. Description of representative profile from the study site. Descriptors for organic horizons follow Klinka et al. (1981).

Horizon	Depth, cm	Description
L	3-2	Loose; dominantly Douglas-fir needles and twigs, salal leaves.
F	2-1	Weakly tenacious; compact matted; few fine roots; abrupt smooth boundary
H	1-0	10YR 2/2; weak granular; felty to fibrous; abundant very fine to fine horizontal roots; clear smooth boundary
Ahe	0-10	10YR 4/2; LS; weak fine to medium subangular blocky; friable; abundant very fine to coarse roots; clear wavy boundary
Bf	10-35	10YR 5/6; LS; weak medium subangular blocky; very friable; plentiful very fine to coarse roots; clear wavy boundary
BC1	35-51	10YR 4/4; LS; single grain; loose; plentiful medium to coarse roots; gradual smooth boundary
BC2	51-80+	10YR 3/4; LS; single grain; loose with occasional durinodes; few coarse roots; abrupt contact with bedrock

locations within the stand and precipitation was measured in a clearing 500 m from the study site.

2.2 Experimental Design

Fifteen 11 x 11 m plots separated by at least 10 m were established at random locations. Three replications of the following treatments were assigned at random:

1. control
2. spring application of ^{15}N-enriched urea (N dosage, 200 kg ha^{-1})
3. fall application of ^{15}N-enriched urea (N dosage, 200 kg ha^{-1})
4. spring application of ammonium nitrate (N dosage, 200 kg ha^{-1})
5. fall application of ammonium nitrate (N dosage, 200 kg ha^{-1})

Powdered urea, enriched at 4.934 atom % excess in ^{15}N, was compressed into granules (approximately 5 mm diameter) by Tennessee Valley Authority, Muscle Shoals, Alabama. On May 21 and November 26, 1982 fertilizers were applied to whole plots from a cyclone seeder while making multiple traverses in alternate directions.

Plot Characterization

Because of variability in the grading and spatial distribution of coarse fragments in the till, it was necessary to determine bulk density on a plot-wise basis. Two excavation methods were used. Pits, approximately 35 cm diameter, were dug within 2 m of each of one or two randomly selected edges per plot. One pit was dug beside plots that had given consistent estimates for coarse fragment contents in the sample cores; generally those where cobble was absent. Two pits were excavated at all other plots. The first 10 cm of soil was excavated and the hole was lined with plastic, then backfilled with water to determine the volume. The water was then removed, the pit extended to 30 cm and the volume determined once more by water displacement in the same way. The volume of the 10-30 cm excavation was calculated as the difference between the second and first volumes. Soil materials were saved by depth, dried at 105 °C and weighed. Because ground selected for bulk density determination was rarely level it was difficult to judge when the excavation was full of water. This potential error was tested for by evaluating volume by the method of Flint and Childs (1984). No differences were found in a paired t-test of volumes by the two methods on a subset of 8 excavations. The water displacement method, which was found more convenient, was therefore used in the remainder of determinations.

The bulk density of the soils, with mass of coarse fragments subtracted, varied from 0.17 to 0.86 Mg m^{-3} (Table 2-2). Most of this variation was explained by variation in the coarse fragment content, which varied from 45 to 91% by mass. The correlation is expected due to the method of expanding fine earths into the volume occupied by coarse fragments. This meant that the bulk density of the fine earth fraction in situ was relatively unaffected by the proportion of coarse fragments. Areas with very high coarse fragment contents were characterized by high proportions of cobble whereas areas with lower contents usually had only pebbles in the coarse fragments. These cobbly areas appeared to have higher organic matter contents in the fine earth fraction and were difficult to sample accurately because the impact corer usually failed to shatter cobbles. This meant that plots 6, 8, 9 and 14 usually required more attempts to obtain cores and those obtained were less satisfactory in terms of the integrity of horizonation. Fortuitously, each fertilizer treatment had only one such plot.

Characterization of Whole and Inner Plots

Because crown diameters were considerable relative to plot dimensions (approximately 5 m vs. 11 m X 11 m) trees near the plot edges were expected to have portions of their root systems outside the plot boundaries. We therefore used a subset of trees within a 5 m radius of plot centre ("inner plots") to generate an accurate estimate of response expected on a stand basis. This constraint eliminated trees in plot corners and reduced the number of individuals per plot by 32% over the experimental area. As inner plots were 35% smaller than whole plots there was no evidence that restricting plot size had biased the spatial distribution of stems. Whole plots had, on average, 13 stems over 10 cm dbh. Initial height, basal area projected from breast height, and volume varied among inner plots (Table 2-3).

Table 2-2. Bulk density *(SD) and coarse fragments by treatment and plot.

		Bulk Density, Mg m^{-3}		Coarse Fragments, % by mass	
Treatment	Plot	0-10 cm	10-40 cm	0-10 cm	10-40 cm
Control	3	0.60	0.58	57	67
	5	0.56 (0.22)	0.62 (0.08)	52	57
	7	0.47 (0.09)	0.48 (0.08)	64	53
Spring Urea	2	0.44 (0.02)	0.52 (0.16)	66	71
	9	0.17 (0.02)	0.36 (0.08)	91	79
	12	0.59 (0.03)	0.54 (0.02)	48	55
Spring AN	1	0.50	0.59	63	64
	6	0.36	0.43	84	74
	13	0.40 (0.01)	0.46 (0.12)	67	66
Fall Urea	10	0.50 (0.01)	0.43 (0.04)	59	64
	14	0.31 (0.08)	0.54 (0.14)	86	54
	15	0.44 (0.02)	0.53 (0.03)	71	69
Fall AN	4	0.56	0.86	48	45
	8	0.24	0.24	77	86
	11	0.56 (0.06)	0.58 (0.03)	59	59

* Bulk Density = oven-dry mass <2mm soil (Mg) / excavation volume (m^3)

Table 2-3. Prefertilization (1982) stand characteristics of trees in inner plots.

Season of Application	Fertilizer Treatment	Plot (# trees)	Height m	Basal Area $m^2\ ha^{-1}$	Volume* $m^3\ ha^{-1}$	Biomass† Mg ha^{-1}
Spring	Control	3 (8)	18.9	35.4	305	209
		5 (7)	20.5	33.2	314	201
		7 (7)	14.2	20.3	136	112
	AN	1 (9)	20.8	48.1	465	298
		6 (6)	16.6	18.3	146	102
		13 (7)	14.5	16.9	115	90
	Urea	2 (7)	17.8	32.8	280	200
		9 (11)	17.8	37.8	321	216
		12 (7)	18.2	30.4	263	181
Fall	Control	3 (8)	19.3	36.0	318	213
		5 (7)	21.1	33.9	331	206
		7 (8)	14.2	22.0	148	121
	AN	4 (6)	22.9	42.0	448	275
		8 (7)	14.6	16.3	117	87
		11 (12)	17.7	42.6	364	247
	Urea	10 (11)	17.6	38.7	313.0	219.8
		14 (8)	19.9	44.5	423	283
		15 (11)	17.8	43.7	366	257

* Volume calculated from the regional equation of Bruce and DeMars (1974)

† Aboveground biomass calculated from the equations of Grier et al. (1984)

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3. VOLATILIZATION AND FOLIAR RECAPTURE OF AMMONIA FOLLOWING SPRING AND FALL APPLICATION OF NITROGEN-15 UREA TO A DOUGLAS-FIR ECOSYSTEM

3.1 Introduction

Urea $[(NH_2)_2CO]$ is the major fertilizer N source in northern temperate agriculture (Fenn and Hossner 1985) and should be a suitable choice for forest applications in view of its ease of handling, low cost of production and high nitrogen analysis. However, growth response to AN has frequently exceeded that from urea in Swedish forests (Holmen 1977), and urea fertilizers have now been almost completely supplanted by ammonium nitrate. Volatilization of NH_3 following application of urea is a well-documented process by which nitrogen may be lost from soil and may partially explain the Swedish results.

Estimates of volatilization losses from forest soils vary from less than 5% (Overrein 1968, Volk 1970) to over 40% (Watkins et al. 1972). The major environmental and edaphic factors affecting NH_3 volatilization have been identified for some time (Ernst and Massey 1960, Watkins et al. 1972), but important questions remain regarding their kinetic effects. For example, rainfall following fertilization generally reduces subsequent volatilization (Carrier and Bernier 1971) but contradictory reports exist (Mahendrappa and Ogden 1973, Craig and Wollum 1982). Effects of simulated rainfall on NH_3 evolution rates have been examined in the field (Marshall and DeBell 1980) and, more commonly, in the greenhouse or laboratory (Bouwmeester et al. 1985) but there is little information on the effects of natural rainfall events and associated humidity fluctuations. Accurate prediction of urea behavior in forest soils is limited by lack of understanding of the manner in which environmental factors affect the intensities of processes leading to volatilization.

A version of this chapter has been published.
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The fate of volatilized NH_3 in forests is not known. It has been assumed that volatilized fertilizer N was lost from the ecosystem. NH_3 evolved from the soil surface may, however, be captured by a plant canopy and possibly assimilated in agro-ecosystems (Denmead et al. 1976, Lemon and Van Houtte 1980). Field evidence for such an intrasystem cycle is lacking for forests but laboratory studies have demonstrated uptake of gaseous NH_3 by excised conifer foliage (Mahendrappa and Ogden 1973, Pang 1984). The partial pressures of NH_3 used in these studies were high, however, and it is not clear how intact coniferous tissues might respond to fluctuating or lower levels expected in the field following fertilization.

The objectives of the present study were to examine the dynamics of NH_3 volatilization under the influence of natural rainfall events following spring and fall urea application and to test the hypothesis that forest vegetation may capture NH_3 from the atmosphere.

3.2 Materials and Methods

The study site, stand characteristics, soils, climate and experimental design are described in Chapter 2. AN treatments were not monitored for NH_3 volatilization and will not be discussed in this chapter.

Throughfall was measured at three locations within the stand whenever volatilization sorber disks were changed - at least 3 times per week. Precipitation was measured in a clearing 500 meters from the study site.

Two weeks after fertilization soils were sampled to a depth of 30 cm using an impact corer (Jurgensen et al. 1972) of 57 mm inner diameter, at nine grid locations established by orthogonal trisection of each plot. Samples were composited within plot by horizon (forest floor) or by 10 cm depth increment (mineral soil). Forest floor samples were air-dried and ground to pass a 2 mm sieve in a Wiley mill. Mineral soils were air-dried and passed through a 2 mm sieve prior to analysis.

Ammonia Volatilization

A square 1 m^2 microplot was randomly located in every quadrant of each main plot. Evolution of NH_3 from the soil surface was monitored at two alternate locations within each microplot.

The semi-open sorber used was based on a design reported by Nômmik (1973a) and described in detail by Marshall and DeBell (1980). The apparatus consisted of a base, sorber chamber and shelter. The base was a 15.3 cm i.d. ABS plastic ring cut into the forest floor. It defined the area over which NH_3 was collected and supported the other parts. The sorber chamber was an ABS cylinder 15 cm tall which fitted tightly to the base and housed two horizontal polyfoam sorber disks which were charged by soaking in 75 mL 0.7 M phosphoric acid in 2.5% glycerol and allowing excess solution to drain under gravity. NH_3 evolved from the soil surface was captured by the lower sorber disk; ambient NH_3 by the upper disk. Such an arrangement permitted interchange of other gases between the chamber and the surrounding atmosphere. The sorber chamber was sheltered from throughfall and litterfall by an inverted, disposable aluminum pie plate.

During fertilization sorber bases were covered with plastic sheets. The plastic was then removed and approximately 9 urea granules were evenly distributed within the bases to achieve the desired application rate. The sorber chambers, equipped with acidified foam disks and shelters, were then positioned on the bases. During the first 14 days following spring fertilization sorber disks were exchanged every two days and thereafter every three days. Road washouts affected site access in fall and resulted in an irregular 2 or 3 day exposure cycle for sorber disks. Each time disks were exchanged the sorber chamber was positioned on the alternate sorber base within the microplot. In this way volatilization rates could be related to the precipitation patterns of the previous two or three days. Exchanged disks were returned to the laboratory for N analyses as described below. Contamination of disks was prevented by use of the procedures suggested by Marshall and DeBell (1980).

Ammonia Recapture

Three 2-year-old Douglas-fir seedlings separately potted in a 1:1 v/v peat-vermiculite mixture were located within 1 m of plot center in the urea treatments prior to fertilization. Two of the seedlings were positioned 10 cm and the third 150 cm above the forest floor. The upper elevation generally exceeded the understory height by 50 to 70 cm. The pots were recharged periodically with distilled water throughout the volatilization monitoring period (43 and 10 days after spring and fall fertilization, respectively).

Laboratory Procedures

Exposed sorber disks were squeezed thoroughly and sequentially extracted with three 150 mL portions of deionized water. All washings were combined and made to 500 mL with deionized water. Ammonium in this solution from control treatments was determined by an automated modification of the indophenol method (Technicon Industrial Systems 1977). Ammonium in solutions from urea treatments was determined by steam distillation into boric acid followed by titration with 0.005 M H_2SO_4 (Keeney and Nelson 1982).

Seedlings were separated into the following tissue classes:

1. leader
2. current foliage
3. one-year-old foliage
4. roots

The seedling tissues and potting mixtures were dried at 65 °C and ground in a Wiley mill to pass a 1 mm mesh sieve. Samples of the ground material were analyzed for total Kjeldahl N (Bremner and Mulvaney 1982).

Mineral nitrogen in soil samples was extracted with 2M KCl (Keeney and Nelson 1982) using a 5:1 or 10:1 solution to soil ratio for mineral soils and forest floors, respectively. The soil residue from extraction was washed with 0.01M KCl, dried, milled to pass a 0.25 mm mesh sieve, and analyzed for total Kjeldahl N (Bremner and Mulvaney 1982).

Titrated distillates from the Kjeldahl determination were acidified with H_2SO_4 and dried at 55 °C in preparation for mass spectrometry. Ammonium sulfate salts were oxidized with LiOBr (Porter and O'Deen 1977) and the 29/28 ratios of the resultant dinitrogen determined in a Micromass 602C dual inlet stable isotope ratio mass spectrometer.

3.3 Results

During the periods of measurement NH_3 evolution from control plots was not detectable. Nitrogen concentrations in the analytical solution of control plots were less than 0.2 mg L^{-1}, which was not different ($P<0.66$) from concentrations in sorber pads which were stored in air-tight plastic bags in the laboratory for two days.

The data from urea-treated plots are segregated into A (enabled on the day of fertilization) and B series sorbers (enabled on the first day sorber sponges were exchanged) because each of these has a unique precipitation history. In particular, when a series was active in monitoring ammonia evolution it was not possible for rainfall to enter. Summation of observations in the A and B series yields an estimate of total volatilization, which averaged 28 kg N ha^{-1} (14% of applied) in spring (Fig. 3-1) and 1.4 kg N ha^{-1} (<1% of applied) in fall (Fig. 3-2). These were statistically different ($P<0.001$) by a t-test of totals within plots.

Both thermal and precipitation regimes following fertilization differed between spring and fall (Figures 3-1 and 3-2). Air temperature averaged 9.2 and 3.1 °C for the two-week period following application of urea in spring and fall, respectively. Throughfall in the same intervals was 16 times greater in fall.

Generally volatilization rates did not correlate with temperature alone. For example the evolution of NH_3 recorded at the A sorbers on the first sampling dates after fertilization (adjusted for the larger sampling period in fall), when no additions of moisture had

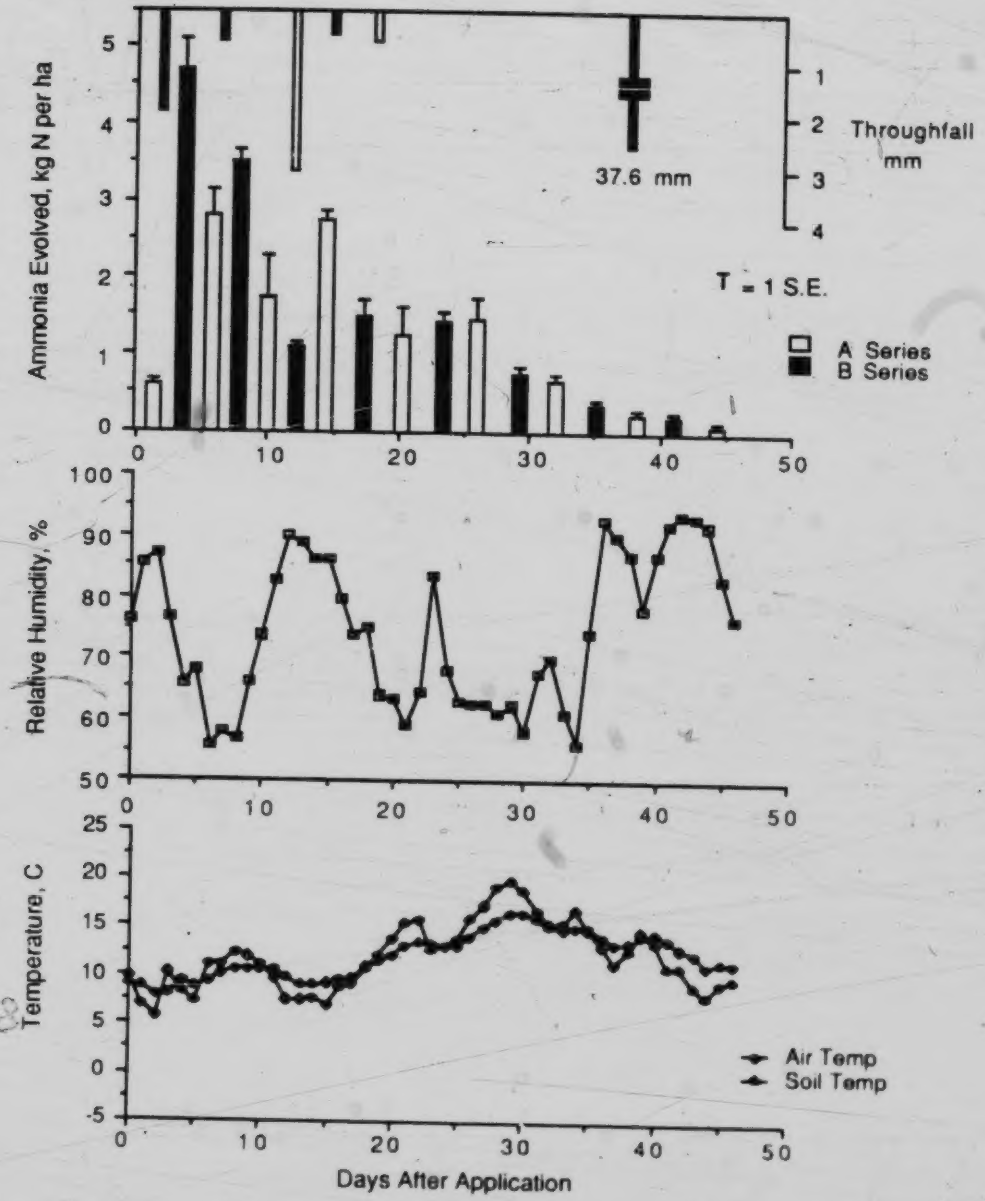

Figure 3-1. Ammonia evolution, precipitation, humidity and temperature following spring application of 200 kg N ha^{-1} as urea to a forest soil. Solid hanging bars in uppermost trace indicate precipitation events affecting "B" series sorbers while hollow hanging bars pertain to "A" series sorbers. Measurement interval for volatilization 2 days initially, increasing to 3 days at day 15.

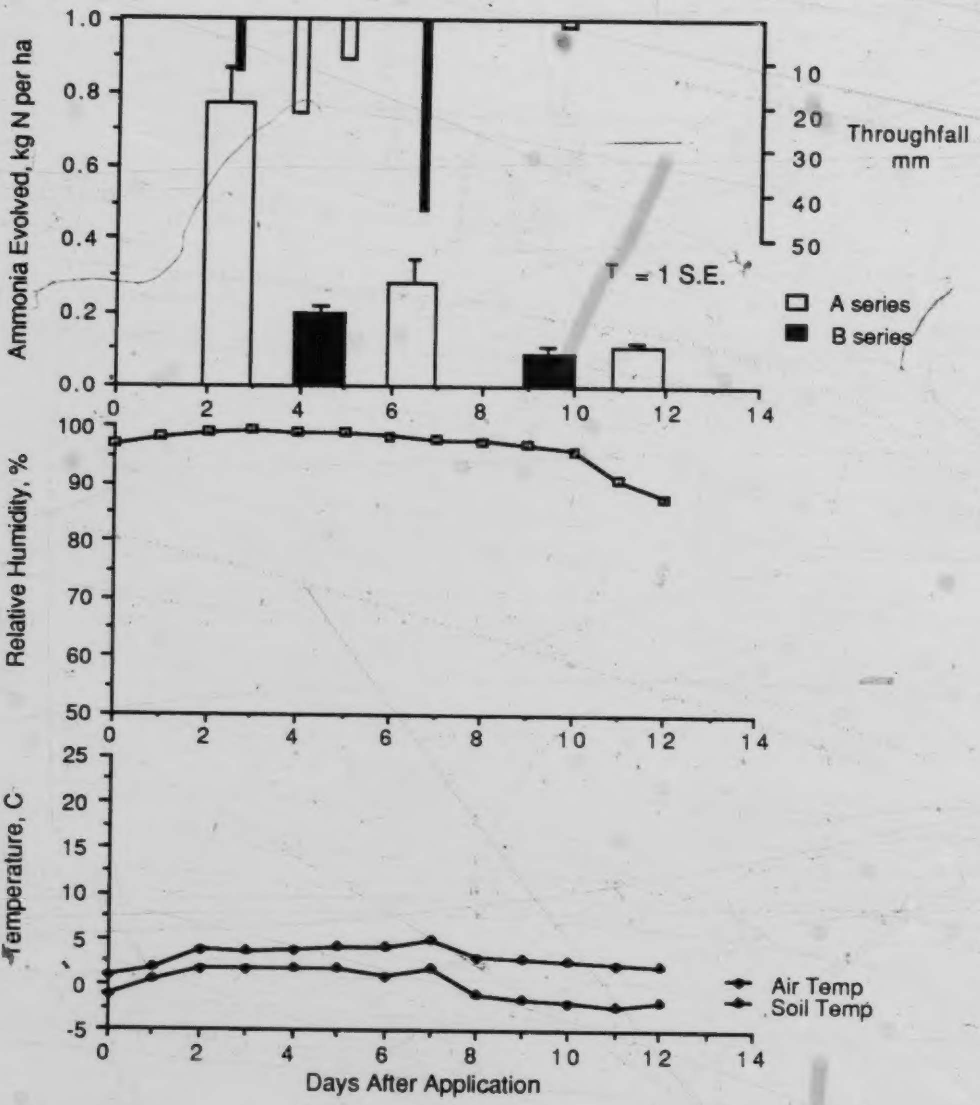

Figure 3-2. Ammonia evolution, precipitation, humidity and temperature following fall application of 200 kg N ha^{-1} as urea to a forest soil. Solid hanging bars in uppermost trace indicate precipitation events affecting "B" series sorbers while hollow bars refer to precipitation affecting "A" sorbers. Measurement interval for volatilization either 2 or 3 days as detailed in Materials and Methods. Note differences in scale from Figure 3-1.

occurred, were similar in spring and fall despite a 10 °C difference in air temperature. No clear pattern on subsequent dates emerged between temperature and NH_3 evolution.

Throughfall, however, appeared to influence volatilization rates. In the first week following spring application only [illegible].9 mm of precipitation reached the forest floor and urea pellets were visible for as long as 6 days in microsites protected from direct throughfall. Total moisture in the forest floor at this time was 5.3 mm which is sufficient to dissolve all urea applied. Precipitation was generally followed by an increase in NH_3 evolution. For example the B series sorbers, which were uncovered during the first rainfall, collected more ammonia than the A series on the first two sampling dates. Small precipitation events on days 13 and 16 were accompanied by pulses of volatilization in the A and B series, respectively. Rainfall events of approximately 0.5 mm on the 7th and 19th days did not produce immediate volatilization increases but each of these was preceeded by a comparatively large rainfall event that probably masked any direct response. By the time a large (38 mm) rainfall occurred at the 40th day, NH_3 evolution rates had already fallen to near control levels.

More than twice as much forest floor moisture was present in fall than in spring (Table 3-1) and small rainfalls on the two days preceding fertilization left the surface of the forest floor wet. With the exception of the first data point, each NH_3 sampling after fall fertilization was influenced by relatively large rainfalls. These depressions in volatilization were associated in every case with moisture additions. The rate of NH_3 evolution was maximal during the first three days and did not differ from that measured under spring fertilization but the rate thereafter was significantly lower ($P<0.05$), averaging 4, 10, 2 and 6% of the spring rates respectively over the remaining four dates.

Within a season there was generally synchronous behavior between the gross NH_3 evolution (Figures 3-1 and 3-2) and the proportion of evolved NH_3 derived from the applied fertilizers (Figures 3-3 and 3-4). Differences occurred in the timing of the peaks, however. For example in spring, evolution of NH_3 reached a maximum 4 days after

Table 3-1. Chemical and physical properties of the study soil

Horizon	Depth	pH†	C‡	N	C/N	Coarse Fragments	Initial Moisture§ Spring	Fall	Texture
	-cm-		---- g kg^{-1} ----			------------ kg kg^{-1} ------------			
Oi/Oe	3-1	3.95	441	7.8	56	-	1.15	2.51	-
Oa	1-0	3.85	295	7.1	41	-			-
A	0-8	4.62	58.3	1.3	46	0.45	0.40	0.39	LS
Bs	8-23	4.70	30.9	0.7	43	0.53	0.32	0.35	LS
BC1	23-49	4.65	25.4	0.6	41	0.52	-	-	LS
BC2	49-80+	4.75	-	-	-	-	-		LS

† pH was determined in 0.01 M $CaCl_2$ using a 1:2.5 or a1:10 soil:solution ratio for mineral soils and organic horizons respectively.

§ Moisture percentage on mass basis for the fine earth fraction.

‡ Includes roots <2 mm diameter

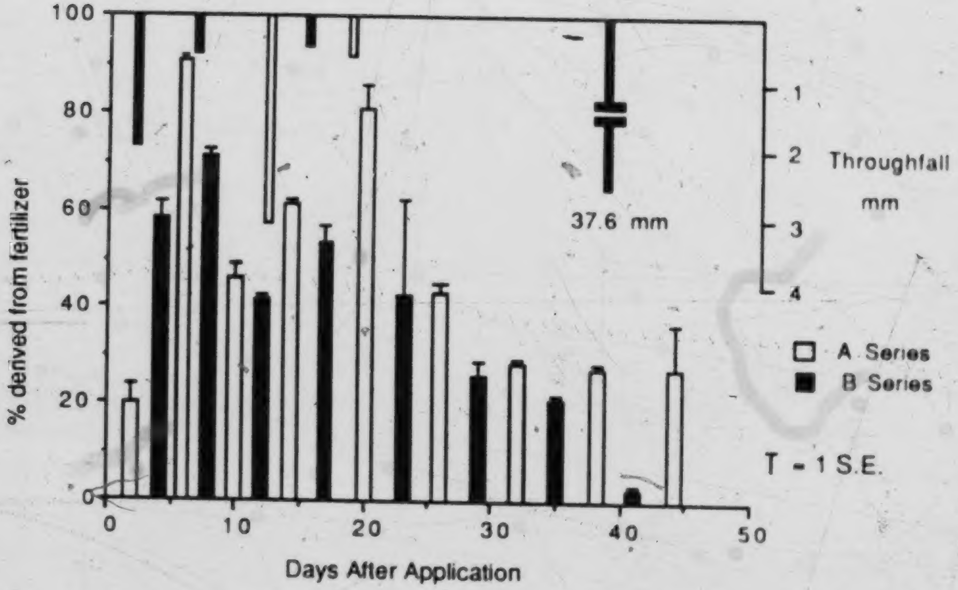

Figure 3-3. Ammonia evolution of fertilizer origin after spring application of pelleted urea at 200 kg N ha^{-1}. Solid hanging bars indicate precipitation events affecting "B" series sorbers while hollow hanging bars relate to "A" series. Measurement interval for volatilization 2 days initially, increasing to 3 days at day 15.

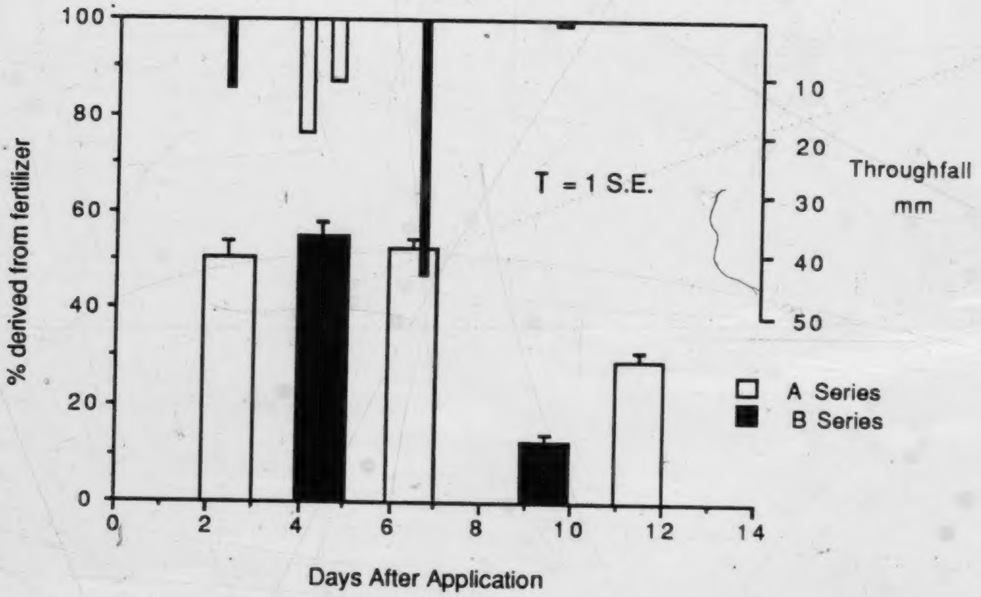

Figure 3-4. Ammonia evolution of fertilizer origin after fall application of pelleted urea at 200 kg N ha^{-1}. Solid hanging bars indicate precipitation events affecting "B" series sorbers while hollow hanging bars relate to "A" series. Measurement interval for volatilization either 2 or 3 days as detailed in Materials and Methods.

application (Fig. 3-1) while the maximum fertilizer proportion was not reached until the 6th day (Fig. 3-3). This maximum arose from the A series sorber which had received no rain to that point in time. A prominent maximum occurred 20 days after application in the A series sorbers. This coincided with a small rainfall which followed the major precipitation input on the 14th day. This precipitation event did not elevate NH_3 evolution, however. Similarly, the rainfall on day 7 affecting the B series produced an increase in the labelling but not the amount, of evolved NH_3.

Recapture of volatilized labelled N by potted Douglas-fir seedlings was detected after spring application of urea (Table 3-2). Tracer N was not merely sorbed to plant surfaces because extraction of intact tissues with 0.005M H_2SO_4 yielded only traces of labelled N. Seedlings positioned 10 cm above the forest floor had a mean ^{15}N excess 16 times greater than that found at the 150 cm elevation and this difference was highly significant ($P<0.01$). The total concentration of N in seedlings from the two elevations also appeared to differ but this is not supported statistically ($P=0.13$). ^{15}N was not allocated equally among seedling tissues. Needles from seedlings at 10 cm elevation had enrichments 2-3 times greater than roots. Current year needles were more enriched than one-year-old needles. Weaker partitioning patterns existed in seedlings positioned at 150 cm. While aboveground tissues were significantly enriched over roots no further differentiation could be made among needles with respect to ^{15}N distribution. Peat potting mixtures at both elevations contained detectable amounts of tracer N. At the lower elevation the ^{15}N excess in the potting mixture was about 20% of that in the roots - the least labelled plant component. At the higher elevation, roots and potting mixture were similarly labelled.

3.4 Discussion

Volatilization Estimation

Fenn and Kissel (1973) demonstrated in the laboratory that air flow rates affect total volatilization by regulating readsorption by soil of volatile NH_3. Maximum and

Table 3-2. Distribution of labelled N in potted Douglas-fir seedlings at two heights above forest floor fertilized in spring with ^{15}N urea. Where brackets occur data are means (standard deviation). Means not followed by the same letter differ at $P \leq 0.05$. Uppercase letters (A, B, C) denote differences between elevations for a component and lowercase letters denote differences among components within an elevation.

	Elevation					
	10 cm			150 cm		
Component	TKN *	^{15}N excess†	PDF‡	TKN	^{15}N excess	PDF
Needles	mg kg^{-1}			mg kg^{-1}		
Leader	20.8 (3.3)	0.215 (0.110)^{Axy}	0.0463	17.4 (0.7)	0.013 (0.004)^{Bx}	0.0028
Current year	18.5 (3.6)	0.280 (0.141)^{Ax}	0.0604	15.2 (3.0)	0.011 (0.002)^{Bxy}	0.0024
1 year old	12.6 (6.7)	0.140 (0.062)^{Ayz}	0.0301	9.8 (1.6)	0.014 (0.001)^{Bx}	0.0031
Roots	11.7 (3.2)	0.073 (0.046)^{Az}	0.0158	10.8 (2.4)	0.006 (0.002)^{By}	0.0014
Peat	2.9 (0.7)	0.015 (0.010)^{Az}	0.0033	3.3 (0.6)	0.005 (0.001)^{Ay}	0.0011

* total Kjeldahl nitrogen
† atom % excess
‡proportion due to fertilizer

reproducible volatilization rates were obtained only when air flow reached 15 to 20 replacement volumes per minute. In the field Marshall and DeBell (1980) also showed a dependence of measured volatilization on gas exchange characteristics of the sampling device. Closed static samplers yielded 25% lower estimates than a semi-open design similar to that used in our study. These authors compared both of the field samplers to a closed, forced circulation laboratory system employing ^{15}N and concluded that although the semi-open design gave the most accurate estimate, even this rate was about 80% of the true rate. Tradeoffs may be involved when attempting simultaneous optimization of reproducibility and accuracy. Fenn and Kissel (1973) maximized both reproducibility and magnitude of volatilization when headspace air was continuously turned over. In closed canopy forests, however, wind velocity at the forest floor may for extended periods be below the threshold for routine measurement. Hence reproducible estimates obtained by high air flow rates cannot necessarily be accepted as accurate measures of the field rate when boundary layers are not permitted to develop. We recognize the limitations on the accuracy of volatilization estimates using the semi-open design but emphasize the value of the data in seasonal comparisons and for examining volatilization dynamics with respect to fluctuating weather conditions.

In this study NH_3 volatilization totalled 0.7 and 14% of applied N in fall and spring, respectively. These rates are within the range cited by Fenn and Hossner (1985) for forest soils and in accord with the general observation that significant post-application rainfall reduces volatilization. The effects of individual precipitation events varied between and, occasionally, within seasons.

Dynamics of Ammonia Evolution

Fall

Visual evidence suggested that fall-applied urea dissolved rapidly and moved into surface horizons. Volatilization rate decreased over time with each rainfall event. Labelling of nitrogen captured in sorber sponges (Fig. 3-3) showed that at no time was NH_3 volatilization solely from fertilizer sources. NH_3 captured in the first measurement period was approximately 50% fertilizer origin, indicating rapid dilution of fertilizer N by native ammonium. Abundant soil moisture coupled with good hydraulic contact between fertilizer pellets and the forest floor apparently were sufficient to cause extensive redistribution of urea. The isotopic abundance of captured N was not altered by rainfalls of 15 mm preceding day 5 and, 22 and 10 mm preceding day 7. This suggests that NH_3 volatilized on the first three dates may have been from a single, homogeneous source. A rainfall of 45 mm preceded the measurement period from day 7 to 10 and the NH_3 collected fell to 17% fertilizer origin. This pattern contrasts with that reported by Marshall and DeBell (1980) from an experiment carried out on a similar soil. In their study pelleted urea was broadcast in fall to provide N at 224 kg ha^{-1} with or without 12 mm of simulated precipitation. The semi-open sorber system they used did not permit further precipitation to reach the soil surface. Under these circumstances measurable volatilization occurred for a period of 41 days. Marshall and DeBell (1980) reported captured NH_3 ranging from an initial 90% to approximately 60% fertilizer origin on the 41st day. Greater dilution of fertilizer N by native ammonium reported in the present study was likely due to redistribution of applied urea caused by the high initial soil moisture content and subsequent precipitation.

The labelling of the NH_4^+-N pool at 3 weeks (Table 3-3) is greater than for any of the NH_3 captured by the sorbers throughout the monitoring period. The first possible explanation is that the NH_3 captured may underestimate the ^{15}N abundance of the NH_3 actually evolved. This would require either: i) significant isotope fractionation during diffusion of NH_3 from the soil surface to the sorber pad; or ii) isotope exchange through soil recapture and re-emission of NH_3. The former situation would be expected to be of concern only when dealing with very small (e.g. per mil) enrichments of ^{15}N and does not pertain here. Recapture of gaseous NH_3 by a generally acidic forest floor is possible. A net reduction of ^{15}N abundance would require a compensatory re-emission after dilution by

Table 3-3. Distribution of labelled N in soil three weeks after spring or fall application of 200 kg N ha^{-1} as urea. Values are means of 3 observations.

	Season							
	Spring				Fall			
Horizon/Depth (cm)	NH_4^+	PDF†	TKN*	PDF	NH_4^+	PDF	TKN	PDF
	mg kg^{-1}		mg kg^{-1}		mg kg^{-1}		mg kg^{-1}	
LF	1870	0.81	7920	0.146	2200	0.63	8980	0.116
H	1430	0.70	6680	0.084	1970	0.65	8890	0.111
0-10	132	0.80	1420	0.060	235	0.76	1230	0.095
10-20	46	0.65	866	0.036	67	0.77	580	0.038
20-30	10	0.21	806	0.011	26	0.69	497	0.023

† PDF - proportion derived from fertilizer
* total Kjeldahl N

native NH_3. But recaptured NH_3 would have to migrate to regions of high pH to be revolatilized. This mechanism would in fact serve to maintain microsite sources of NH_3 at a higher ^{15}N abundance than in the absence of gaseous recycling and therefore cannot explain the anomalously low ^{15}N abundance.

A second explanation for the low ^{15}N abundance of captured NH_3 is that it accurately represents the state of the NH_4^+-N pool at the time of volatilization - ie. the pool was never more than 55% fertilizer origin throughout the 2 week measurement period. The extensive dilution of urea-N required for this condition to be met would entail sluggish ureolysis, liberation of large amounts of previously unavailable ammoniacal N, or both. Several researchers have reported that ureolysis in coniferous forest floor materials is rapid (Roberge and Knowles 1966, Overrein 1968) and generally complete within 3 days when sufficient moisture is present for rapid dissolution. Furthermore, redistribution of urea is expected from the high soil moisture content and should promote contact between enzyme and substrate. Hence slow ureolysis does not seem likely to explain the results.

Comparison of unlabelled, extractable NH_4^+-N levels in Oi/Oe horizons of control and urea treatments (data not presented) reveals that, at 3 weeks after application there was an increase from 25 to 816 mg kg^{-1} N. As dramatic as this "priming effect" is, it is still insufficient to explain the dilution of fertilizer N seen in the sorbers. This leads to an interesting hypothesis: microsites of volatilization are distinct from microsites of urea dissolution and hydrolysis.

Spring

When urea was applied in spring patterns of NH_3 evolution were more complex due to the apparent sensitivity of the process to fluctuations in soil moisture at higher tensions. Generally, dissolution and hydrolysis of urea depended strongly on trace precipitation episodes. Small rainfalls were usually followed by a surge in the volatilization rate. Similar effects have been reported by Mahendrappa and Ogden (1973) and Craig and Wollum

(1982) for forest soils and by Titko et al. (1987) in a turfgrass system. Craig and Wollum (1982) noted that small rainfalls (<5 mm) promoted volatilization whereas larger rainfalls had a depressing effect. While our spring volatilization rate usually rose following precipitation the ^{15}N abundance of captured NH_3 was always increased by rainfall. This contrasts with the fall situation where large rainfalls either did not affect or depressed the fertilizer N content of evolved NH_3. Flushes of volatile NH_3 in response to minor precipitation may result from improvement of access between urease and its substrate under dry spring conditions.

Visible persistence of urea pellets after 6 days was evidence that dissolution may have limited the rate of ureolysis. Initially then, urea pellets existed in discrete domains in poor hydraulic contact with the soil. Movement of dissolved urea to sites of urease activity was a dominantly diffusive process because no significant percolation of rainwater occurred until near the end of the measurement period. Dissolution/diffusion episodes leading to improved contact between urea and urease as described above should always produce bursts of volatilization. This was not always observed. In particular the 1 mm throughfall on the 7th day elevated the ^{15}N abundance but not the amount of volatilized NH_3. A similar phenomenon occurred on the 19th day although it is not known if unhydrolyzed urea remained at this time. These observations closely followed larger rainfall events and can be explained by the presence of extraordinarily high concentrations of urea surrounding pellets caused by pulse dissolution. Rachhpal-Singh and Nye (1984) have calculated that concentrations as high as 10M may exist around dissolving urea granules. Urease activity in such zones is likely to be inhibited.

Inhibition of urease in the presence of high concentrations of urea could occur in at least three ways. First, hydrolysis of urea to ammonium carbonate could create zones of pH beyond the optimum for the enzyme. pH optima for soil urease have been reported in the range of 6 to 9 (Mulvaney and Bremner 1981) but a majority of estimates fall between 6.5 and 7.0. Recent work by Rachhpal-Singh and Nye (1984) using an unbuffered assay system showed a 50% reduction in urease activity when the pH was raised from 6.4 to 7.8. Second, in forest floor materials pH surges resulting from urea hydrolysis can result in extraction of considerable organic matter (Roberge and Knowles 1966, Overrein 1968, Otchere-Boateng and Ballard 1978). This could cause release from humic materials of aromatics which strongly inhibit urease (Bremner and Douglas 1971). Extraction of organic matter may also extract and denature urease itself if the proposals of Pettit et al. (1976) are correct. Finally, substrate inhibition has been reported for this enzyme in vitro (Laidler and Hoare 1949) and recently in soil (Rachhpal-Singh and Nye 1984, Monreal et al. 1986). Thus it might be expected that maximum rates of ureolysis will occur towards the urea diffusion front rather than at the pellet itself.

We propose that under the conditions prevailing in spring, urea volatilization patterns were influenced by negative feedback from dissolution rate to ureolysis. Precipitation events induced pulses of dissolution and diffusion of urea into the forest floor. It is likely that urease in the immediate vicinity of urea pellets was exposed to urea concentrations sufficiently high to cause significant substrate inhibition of the enzyme. Further, alkalinity released upon ureolysis may have served as a negative feedback on ureolytic rate by raising the pH past the optimum and possibly altering kinetic parameters (Rachhpal-Singh and Nye 1984). NH_3 released by ureolysis diffused to the soil surface where passage to the atmosphere occurred when sufficient alkalinity was present. Here also feedback occurred as a result of acidification of the solution when NH_3 volatilizes (Vlek and Stumpe 1978). Introduction of small amounts of moisture, then, can be expected to induce an episode of volatilization whose duration is, in part, self-regulated.

The foregoing volatilization scenario is consistent with the observation of increases in ^{15}N abundance each time a small rainfall occurred. Furthermore, it is not inconsistent with the failure of very small rainfall events on the 7th and 19th days to produce an increase in volatilization rate. In these instances the ureolytic-volatilization system had just been strongly stimulated and feedback mechanisms responsible for subduing NH_3 evolution rate were likely operative.

Patterns of NH_3 evolution seen in this study are consistent with the notion that control over volatilization resides in the dynamics of urea dissolution and hydrolysis (Nômmik 1973b, Mahendrappa and Salonius 1974, Reynolds and Wolf 1987). These processes were, in turn, related to the moderation by precipitation of spatial heterogeneity of urea and urease. Further studies on the distribution and activity of urease in forest soils are required before adequate understanding of NH_3 volatilization dynamics will be achieved.

Fate of Volatile Ammonia - Uptake by Seedlings

Based on the mean ^{15}N excess in all plant tissues we calculated that plants at 10 cm elevation took up volatilized N at 16 times the rate of those at 150 cm. Presumably this reflects the average concentration profile during the volatilization period. These data are consistent with daytime NH_3 profiles reported by Denmead et al. (1976) within a ryegrass-sub clover canopy. Harper et al. (1983) and Black et al. (1985) have reported similar profiles above urea-fertilized pastures in Australia and New Zealand. These researchers calculated NH_3 flux densities by micrometeorological techniques and generally found exponential reduction of NH_3 concentration with elevation.

Porter et al. (1972) demonstrated foliar capture and anabolic incorporation of $^{15}NH_3$ by corn plants from atmospheres ranging in NH_3 concentration from 1 to 20 ppm. Hutchinson et al. (1972) showed uptake of NH_3 by soybeans exposed to more typical atmospheric concentrations (≈0.02 ppm NH_3). Excised shoots of Douglas-fir also incorporated $^{15}NH_3$ in atmospheres of 0.03 to 1.09 volume % NH_3 (Pang 1984). We calculate that the NH_3 concentrations used by Pang (1984) are several orders of magnitude greater than those reported by Porter et al. (1972) and Hutchinson et al. (1972). Therefore comparison of relative capture efficiencies of the plants is difficult. Direct evidence of gaseous NH_3 uptake by forest species in the field has not been shown before to our knowledge. The maximum NH_3 evolution rate measured in the present study was 4.7 kg N·ha^{-1} in 2 days. Assuming complete mixing of this NH_3 into a volume extending 1 m above the forest floor over an area of 1 ha, a concentration of 0.07 volume % may be calculated. The atmosphere above the forest floor is an open system and both NH_3 diffusion gradients and wind currents would have served to depress the concentration experienced by plant tissues. Thus, it is expected that NH_3 concentrations in this study were lower than the minimum reported by Pang (1984).

The fact that labelled nitrogen was not distributed uniformly across various tissues is consistent with the proposal of metabolic incorporation followed by rapid redistribution. The relative sink strength observed, current foliage>one-year-old foliage>roots is the same as reported by van den Driessche (1971) for root-derived ^{15}N in Douglas-fir seedlings. There is little doubt that the potential exists for direct foliar uptake of NH_3 by Douglas-fir following urea fertilization. However, the concentration profiles reported by Denmead (1976), Harper et al. (1983) and Black et al. (1985) together with the elevation-uptake data presented here suggest that in Douglas-fir with live crowns at 10 m height, NH_3 capture is likely to be minimal. Foliar uptake of NH_3 is more likely in the herb and shrub layers.

Accurate estimation of the total extent of plant recapture of volatilized NH_3 would require knowledge of NH_3 concentration profiles, kinetics of uptake for the species involved, and leaf area index. While these are not currently available, a crude estimate may be derived from consideration of a hypothetical understory of Douglas-fir seedlings with a crown midpoint elevation of 35 cm and leaf area index of 1. Under these assumptions we may calculate from our spring treatment data that between 8 and 19% of volatilized NH_3 (corresponding to captured NH_3 labelled at 92 and 40% of the fertilizer source, respectively) could be expected in the seedling tissues examined. Additional captured N would be expected in unanalyzed stems and branchwood thereby elevating recovery of volatile N. The actual recapture efficiency will remain speculation, however, until NH_3

compensation points (Lemon and Van Houtte 1980) are determined for Douglas-fir and its understory associates.

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4. DYNAMICS OF FOLIAR N IN DOUGLAS-FIR. I. COMPARATIVE EFFECTS OF SPRING- AND FALL-APPLICATION OF AMMONIUM NITRATE AND UREA.

4.1 Introduction

Trials conducted throughout the Pacific Northwest have shown growth of Douglas-fir to be N-limited. Coastal Douglas-fir stands require N at annual rates of 50 to 70 kg ha^{-1} but frequently these levels are not available (Gessel and Cole 1973). A regional response to N fertilization averages 18% in merchantable basal area over a 10 year period (Gessel 1984); however, considerable variation occurs. Reported growth responses range from slight retardation to significant enhancement extending beyond 10 years (Binkley and Reid 1985). Variability in response to N fertilization can be attributed in part to stand and site factors (Edmonds and Hsiang 1987), however, an adequate mechanism-based explanation of these results has not yet been achieved.

Evidence is accumulating that aboveground growth of coniferous forest trees is closely related to the nitrogen content of the foliage (Brix 1981a, Ingestad and Kähr 1985). Ågren (1983) has proposed that growth can be described as the product of foliar N and the nitrogen productivity, a genetically and phenologically-dependent proportionality coefficient. The level of foliar N ultimately is determined by the rate of N uptake from soil. This rate, in turn, depends on the soil N flux density (Ingestad 1988) and the efficiency of the root system. The variable growth response of Douglas-fir to N fertilization might be related to variability in fertilizer efficiency, reflected in variable enhancements in foliar N.

Successful fertilization will synchronize increases in N availability with periods of maximum uptake efficiency. Generally, uptake of nutrients is most rapid during periods of active root growth when little suberization of recently-formed roots has occurred (Bowen

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1984). Periods of active formation of short lateral roots in early spring and fall have been reported for a number of conifers (Vogt et al 1981, Keyes and Grier 1981, Ford and Deans 1977). From a standpoint of N uptake, spring and fall are similar periods in the Douglas-fir region in that moisture, temperature and root activity are favourable. Nevertheless, the phenological stage of the tree is very different in these two seasons.

Although N fertilization of Douglas-fir has been performed in every season, very few studies have compared seasons of application directly. Heilman et al. (1982) reported higher recovery of fall-, versus spring-applied urea-N in 7 and 9-year-old Douglas-fir. Miller et al. (1986), working with a high-productivity, closed-canopy Douglas-fir stand on Vancouver Island, found higher concentrations of N in current foliage after urea fertilization in fall but ammonium nitrate (AN) yielded higher values when spring-applied.

Availability of fertilizer N is influenced by the chemical source. Ammonium nitrate and urea are the most commonly used sources in forest applications (Ballard 1984). Ammonium nitrate has been used extensively in Scandinavia (Holmen 1977) and has potential for use in the Pacific Northwest but the susceptibility of nitrate to leaching (Overrein 1969) has concerned forest managers. In the Pacific Northwest, urea has been the preferred N source, perhaps due to its ease of handling and high N percentage. Ammonia volatilization is a well-known potential difficulty when urea is used as a fertilizer. Reactions of urea-N with soil organic matter (Nômmik 1982, Foster et al. 1985) may also be a source of poor efficiency. Comparisons between AN and urea conducted in Sweden showed better growth response for AN, particularly for Scots pine at moderate application rates (Malm and Möller 1975). Studies in North America have produced similar results for Douglas-fir (Miller and Reukema 1974, Dangerfield and Brix 1981, Harrington and Miller 1979) but there are also reports indicating no difference between urea and AN (Miller and Harrington 1979, Miller et al. 1986).

Most reports on conifer response to N fertilization have focussed on codominant and dominant members of the stand. However, Miller and Pienaar (1973), Lee (1974) and

Barclay et al. (1982) have all reported increased mortality in small diameter classes of Douglas-fir when fertilized with N. Increased mortality probably involves accelerated shading by larger trees but nutrient uptake differences may occur also.

This paper reports on part of a larger study of N dynamics in a Douglas-fir forest. The specific objectives of the present work were to evaluate N uptake, as recorded in foliage, by Douglas-fir in different crown classes under spring- and fall-applications of both AN and urea. It was hypothesized that N uptake from ammonium nitrate would be greater when spring-applied because higher rates of root growth (Keyes and Grier 1981) and generally lower precipitation rates should minimize nitrate leaching and thereby improve availability to trees. Conversely, urea efficiency was hypothesized to be greater when fall-applied because lower temperatures and more abundant moisture should minimize volatilization and reduce the rate of reactions between urea-derived N and soil organic matter.

4.2 Materials and Methods

The study site, soils, vegetation, climate and experimental design are described in Chapter 2.

Foliage Collection

Foliar samples were obtained from the 4th through the 7th whorl from the top of all trees >10 cm (diameter breast height (dbh)) by use of pole pruners after climbing to a mid-crown position. Portions of branch distal to the bole containing at least two year classes of foliage, including the current year, were taken from three separate branches while avoiding foliage which did not receive full illumination at sometime diurnally, e.g. north aspect. Foliage for a tree was then composited by age using visually equal amounts from the three branches. Samples were dried at 65 °C for 48 hr prior to segregation of needles from branchlets. Details of the timing of sampling and age classes of foliage analyzed are presented in Table 4-1. Sampling was designed to provide frequent observations in the first year (expected to be the most dynamic with respect to foliar N concentrations) and

Table 4-1. Timetable for foliar sampling. Years indicate foliar cohorts taken at a particular sampling.

	Time after treatment Weeks		Treatment				
Date	Spring-applied	Fall-applied	Control	Spring Urea	Spring AN	Fall Urea	Fall AN
May 15/82	-1	-	1981*	1981*	1981*	-	-
June 4	2	-	1981	1981	1981	-	-
July 20	9	-	1981, 82	1981, 82	-	-	-
Nov 15	-	-1	1982*	-	-	1982*	1982*
Dec 17	30	3	1981, 82*	1981, 82*	1981, 82*	1982	1982
May 30/83	53	28	1982, 83	1982, 83	1982, 83	1982, 83	1982, 83
Nov 26	79	52	1982, 83*	1982, 83	-	1982, 83*	1982, 83*
May 25/84	105	78	1983	1983	1983	1983	-
Nov 26	-	104	1983, 84	-	-	1983, 84	1983, 84

*Mean needle mass determined on selected trees.

thereafter give information on conditions at inception and maturation of new cohorts of foliage.

Laboratory Procedures

On dates given in Table 4-1, masses were determined on ten samples of 80 dried needles drawn at random from needle composites of selected trees. Dried foliage which had been segregated from branchlets was ground in a Wiley mill to pass a 1 mm sieve. Samples of the ground material were digested using a modification of the sulfuric acid/peroxide method of Thomas et al. (1967). N in the digests was determined on an AutoAnalyzer (Technicon Industrial Systems 1977). Ammonium in the digests was recovered for mass spectrometry by steam distillation into dilute boric acid.

Data Analysis

A multivariate analysis of variance (MANOVA) procedure in the MGLH module of SYSTAT (Systat Inc. 1986) was used to perform profile analysis of repeated measures on the plot means of foliar masses, nutrient concentrations and contents (Morrison 1976). The profile analysis procedure is analogous to the univariate split-plot procedure commonly used in that, examination of effects proceeds from the interaction of main and split factors to the main effects. Effects, however, are tested with hypothesis (H) and error (E) sums of squares and cross-products matrices rather than mean squares (Morrison 1976). This means that there is no scalar equivalent to F in the univariate ANOVA. Rather, the result is a matrix whose degree of dispersion is related to the probability of rejecting the hypothesis. The hypothesis is evaluated from statistics that are based on eigenvalues extracted from the test matrix (HE^{-1}). Of the common test statistics the most robust to departures from multinormal assumptions is Pillai's Trace (SPSSX User's Guide 1986):

$$V=\sum_{i=1}^{s}\frac{1}{1+\lambda_i} \qquad [1]$$

where λ_i = i^{th} eigenvalue of test matrix

s=# of non-zero eigenvalues of HE^{-1}

An approximate transformation of Pillai's Trace to the F-distribution (Pillai 1960) available in SYSTAT (SYSTAT Inc. 1986) was used.

After current foliage had reached maturity in fall it was assumed for the purpose of calculating N content of needles that the unit weight did not change over the following 18 months (Smith et al. 1981). Nitrogen contents of needles were calculated for plots by summing for individual trees the product of needle mass and N concentration. Planned orthogonal contrasts were used to indicate differences between control and fertilized treatments on selected dates. The constrasts used were: 1) fertilized vs control and 2: urea vs AN. Where increments over control are presented they were calculated by subtracting the mean of all control plots from individual fertilized plot means. The significance level for comparisons was set at 0.1.

It is possible to make relevant comparisons of nutrient mass because of the determinate growth of Douglas-fir (Allen and Owens 1972). In this study 1982 foliage (spring treatments) and 1983 foliage (fall treatments) gave reliable nutrient content information because the primordia for shoots had been formed prior to fertilization. The nutrient status of foliage classes newer than these are less informative because vegetative bud primordia are formed under the elevated nutrient regime. Brix (1981b) has shown that Douglas-fir response in second and third years after fertilization is characterized by an increase in both shoot numbers and number of needles per shoot. Thus, response could be said to be expressed at the tree level rather than the needle level after a full growing season. With this in mind the power of measurements at the needle level is reduced in years subsequent to the first growing season. Needle masses were thus not determined beyond these times.

4.3 Results

Spring Application

Inner Plots

Peak N concentrations occurred in mid-December 1982, 30 weeks after fertilizer application (Fig. 4-1a). A fertilizer by date interaction, significant at the 0.1 level by F transformation of Pillai's Trace indicated that fertilizer N had been assimilated. The interaction term had a strong quadratic trend component that, by inspection of the magnitude of differences between fertilized and control trees over time (Fig. 4-1a), can be interpreted as reflecting fertilizer N uptake on the rising leg of the difference curve followed by redistribution on the declining leg. Maximum elevation of N concentration in fertilized trees occurred also in mid-December 1982 with a 30 and 21% enhancement over control for the ammonium nitrate (AN) and urea sources respectively. Orthogonal contrasts between treatments within dates showed that after 53 weeks the probability of a response in foliar N concentrations had declined to 0.22.

Comparison of N concentrations in one-year-old foliage was made on three dates for urea treatment and one date for AN (Fig. 4-1b). Maximum response to fertilization in foliar N concentrations again was recorded after 30 weeks (mid-December) with increases, significant by contrast, of 23 and 18% over control for AN and urea respectively. On this occasion N concentrations in AN and urea-treated trees were statistically different.

Whole Plots

Analysis of N concentrations in current foliage of the whole plot trees gave generally similar conclusions to those derived from the constrained data. Maximum increment over control in foliar N concentration was detected after 30 weeks (Fig. 4-1c); however, these increments were smaller than for the inner plot dataset (24 and 18% increases for AN and urea respectively, compared to 30 and 21% in the inner plot). The fertilizer by date

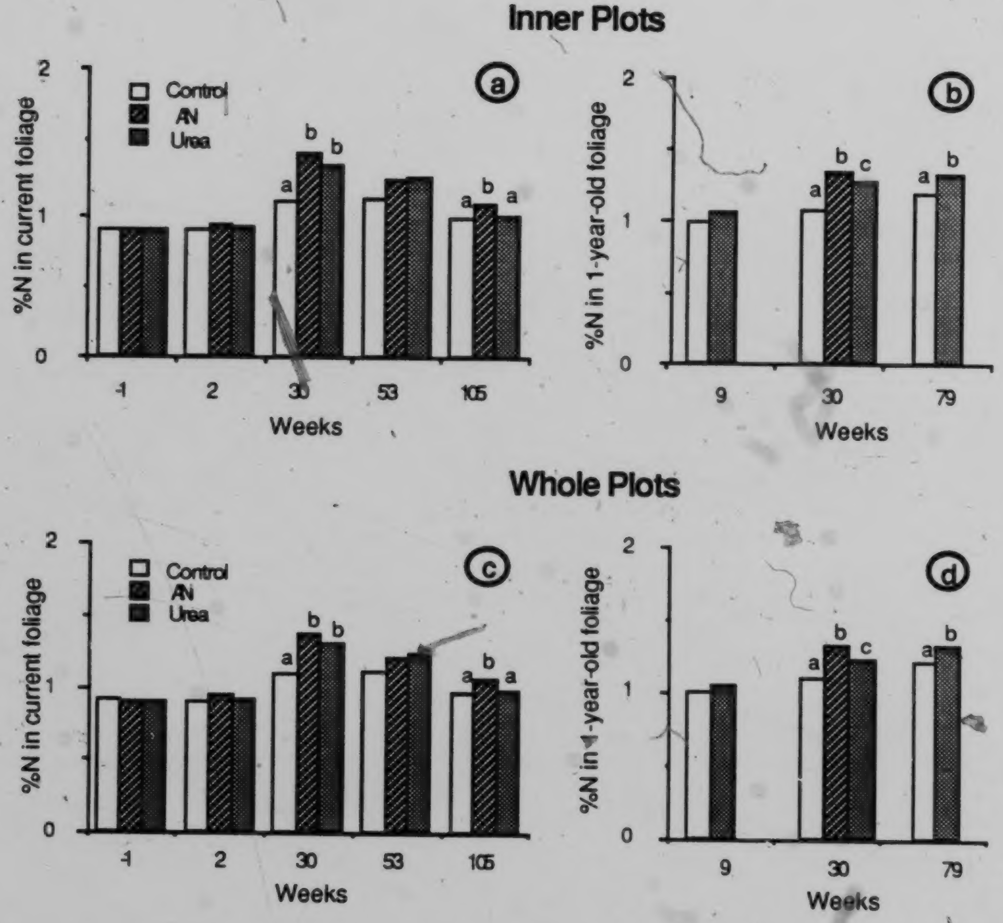

Figure 4-1. N concentrations in two age classes of Douglas-fir foliage after spring application of N @ 200 kg ha^{-1} as ammonium nitrate (AN) or urea. Whole and inner plots defined in Results. Different lowercase letters indicate significant contrasts ($P<0.1$) among treatments on a given date. Numbers above histogram columns refer to year that foliage flushed.

interaction was more distinct than for inner plots ($P \leq 0.01$) and 54% of the variation could be explained by a quadratic trend.

Analysis of whole plot trees for N concentrations in one-year-old foliage (Fig. 4-1d) yielded similar results when compared to the constrained data. Enhancements of 18 and 23% in N concentration in one-year-old foliage after 30 weeks for AN and urea treatments respectively, fell to 13 and 21% when all trees were included. It was generally true that trends in the inner plots were present also in the whole plots. The magnitude of differences among treatments was usually greater in inner plots but the significance of the differences was more often diminished - particularly in the case of orthogonal polynomials. This pattern was attributable to lower error variances when a larger sample of trees was used. For this reason we have made general use of whole plot data in the following comparisons.

Urea treatments were sampled more frequently (Table 4-1), which permitted a more detailed profile of current-year foliar N concentrations for spring urea application (data not shown). Inclusion of the two additional dates resulted in a strong fertilizer by date interaction ($P \leq 0.003$) in which 78% of the variation was accounted for by a quadratic trend. As noted for both fertilizer sources the peak response in N concentration occurred in late fall, 30 weeks after application.

The disposition of N in whole plots between current and one-year-old foliage of fertilized trees is presented in Figure 4-2. The additional comparison at 53 weeks was made by designating 1982 foliage as one-year-old and including an unexpectedly early 1983 flush as current foliage. The absolute levels of nutrients in such tissues are difficult to interpret because of rapid fluctuations accompanying elongation and hardening of shoots. Thus the data are presented only as increment over control. Larger enhancements of N occurred in younger foliage during the first year after fertilization. For the urea treatment, the N increment in current foliage was 40% greater than in one-year-old foliage at 30 weeks and 63% greater at 53 weeks. On the same dates the AN treatment had N increments 19 and

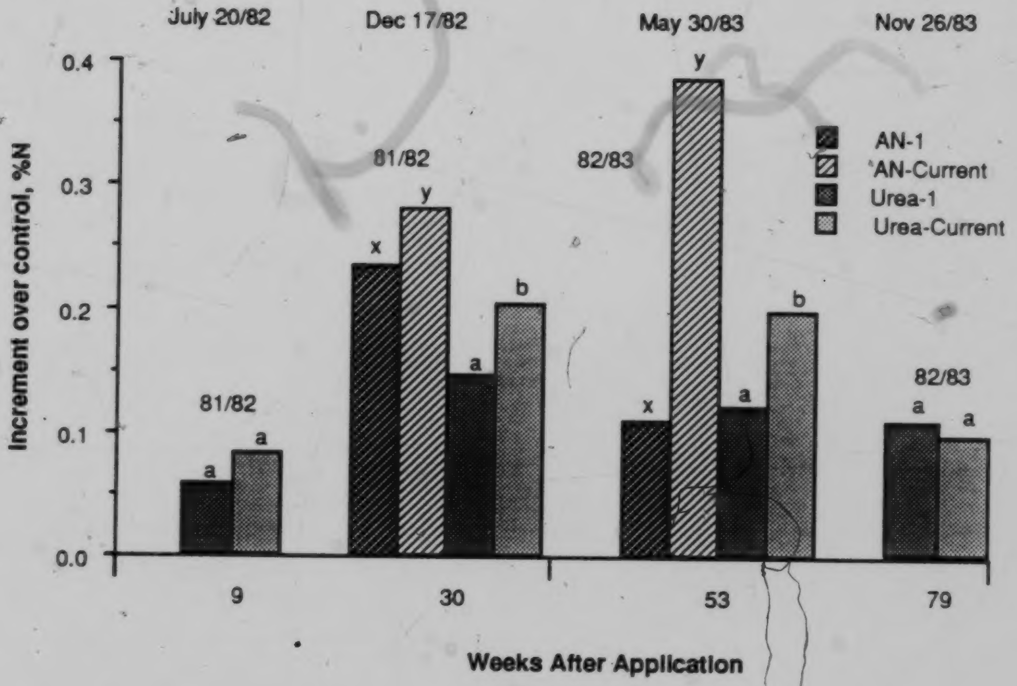

Figure 4-2. Enhancement of nitrogen percentage over control in current and one-year-old foliage at four dates following spring application of AN or urea to Douglas-fir. Lowercase letters indicate differences (P<0.10) within a fertilizer source. Numbers refer to year in which foliage flushed.

351% greater in current than in one-year-old foliage. This suggested a preferential allocation of fertilizer N to younger foliage. This is not borne out by the ^{15}N data.

Effects Within Crown Class

Trees were classified as dominant/codominant or intermediate/suppressed by examining the frequency distribution of tree heights within plots. This two-category classification was used to split the dataset and the resultant subsets were analyzed for trends in foliar N concentrations as presented for the full dataset. Mensurational characteristics of treatment groups and their crown class subsets are given in Table 4-2.

Comparisons of AN with urea for N concentrations in current foliage as increment over control within crown classes generally coincided with results obtained for whole plots but significant differences were larger for the dominant/codominant trees and smaller for the intermediate group (Table 4-3). The effects of constraining the dataset were broadly additive. For example, current foliage N levels for AN-treated trees 30 weeks after fertilization averaged 25% above control, and constraining this group enhanced by 3 and 5% for dominant-codominant and inner plot respectively; while the doubly constrained group had N levels 33% above control.

Current foliar N enhancements declined over the period 6 months to 24 months after fertilization (Table 4-3). Two years after fertilization all subsets of the urea treatment had foliar N concentrations similar to control. By contrast most subsets of the AN treatment exhibited approximately 10% enhancements over control, with significance levels near 0.1.

Fall Application

Inner Plots

N concentrations in current foliage of all treatments changed over time as indicated by a significant multivariate test statistic. Linear and quadratic trends accounted for a similar proportion of the variance associated with this main effect. The peak foliar N concentration occurred after 28 weeks in the AN treatment (Fig. 4-3a). At this time the urea treatment did

Table 4-2. Mean (± standard deviation) tree mensurational characteristics of crown classes.

Treatment	Class Boundary Height (m)	Crown Class: Dominant/Codominant dbh (cm)	height (m)	n[a]	Intermediate/Suppressed dbh (cm)	height (m)	n
Control	18.0	22.2 (4.3)	19.3 (2.8)	5	17.2 (4.3)	16.3 (3.6)	7
Spring AN	17.0	20.9 (4.4)	18.6 (2.9)	6	15.7 (4.9)	15.3 (3.6)	6
Spring Urea	18.0	22.9 (2.7)	20.0 (1.3)	8	16.6 (2.8)	16.2 (1.5)	6
Fall AN	17.7	22.6 (4.6)	20.1 (2.8)	8	14.1 (3.3)	15.8 (2.8)	5
Fall Urea	17.3	22.4 (4.4)	19.4 (1.9)	9	15.5 (2.1)	16.0 (1.5)	5

[a] average number of individuals in crown class on whole plot basis

Table 4-3. Increment over control (%) in N concentrations of current foliage after spring application of N @ 200 kg ha^{-1} as AN or urea.

		Weeks after application							
Trees included	Source	30 (Dec 17/82)		53 (May 30/83)		79 (Nov 26/83)		105 (May 25/84)	
WHOLE PLOT	AN	24.6*	0.002*	9.3	0.426	-	-	9.1	0.107
	Urea	18.4	0.009	10.9	0.356	8.5	0.104	1.0	0.83
Dom/Codom	AN	27.8	0.007	12.1	0.379	-	-	10.4	0.119
	Urea	21.3	0.021	10.3	0.448	6.3	0.321	3.8	0.523
Intermediate	AN	19.8	0.001	6.0	0.563	-	-	8.4	0.083
	Urea	15.4	0.004	13.1	0.231	11.5	0.029	-0.9	0.832
INNER PLOT	AN	29.6	0.006	12.9	0.284	-	-	10.4	0.074
	Urea	21.4	0.024	13.4	0.268	11.0	0.090	3.1	0.544
Dom/Codom	AN	33.1	0.008	15.6	0.296	-	-	12.8	0.122
	Urea	26.2	0.021	12.5	0.395	11.2	0.280	9.2	0.249
Intermediate	AN	25.5	0.024	11.3	0.243	-	-	-14.6	0.005
	Urea	18.6	0.072	15.5	0.125	13.1	0.036	-0.9	0.810

* Data pairs under a date are %increment, followed by probability of making a Type I error when difference from control is declared.

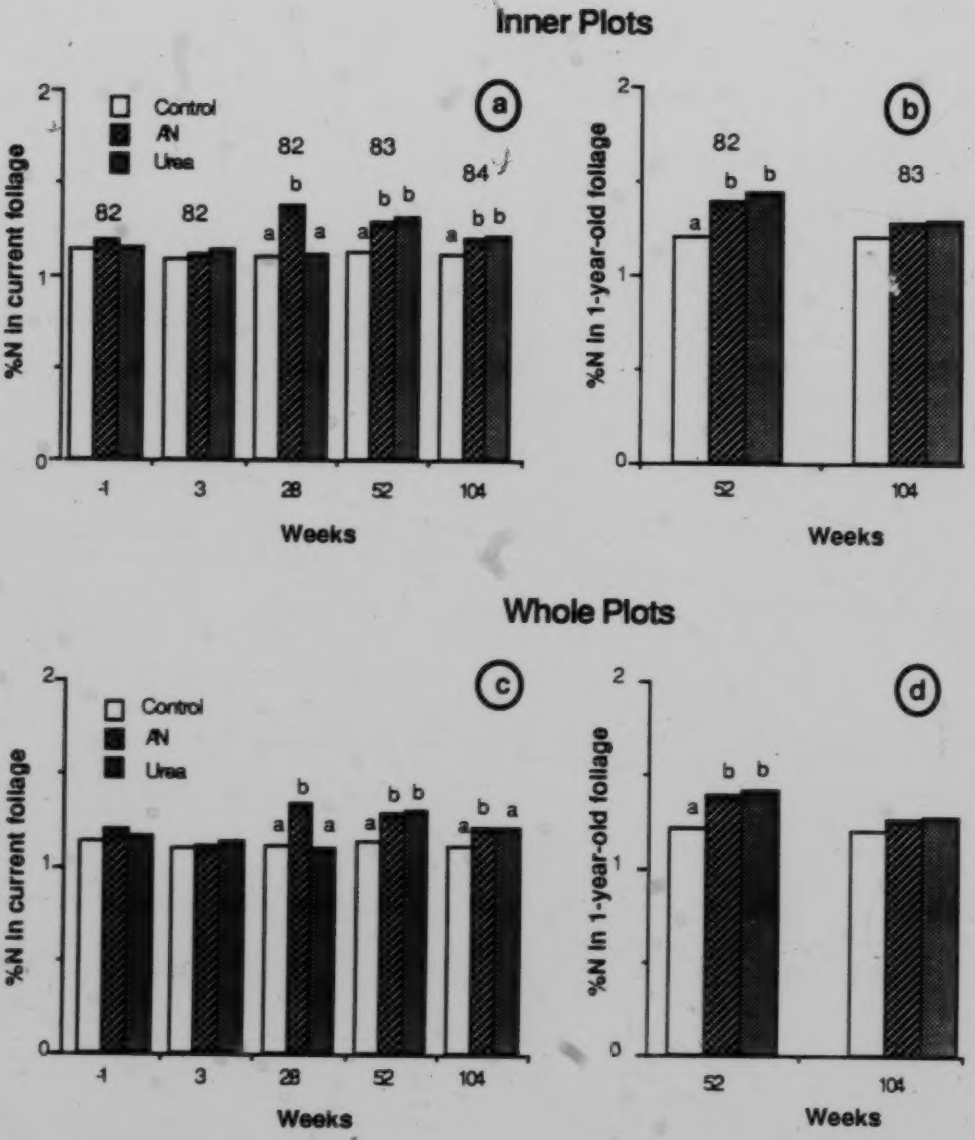

Figure 4-3. N concentrations in two age classes of Douglas-fir foliage after fall application of N @ 200 kg ha^{-1} as ammonium nitrate (AN) or urea. Whole and inner plots defined in Results. Lowercase letters indicate significant contrasts ($P<0.1$). Numbers above histogram columns refer to year that foliage flushed.

not differ from control. Orthogonal contrasts between fertilizer sources within dates showed a significant increment over control for both sources after 52 weeks on November 26/83.

One-year-old needles were analyzed for N concentration one and two years after fertilizer application (Fig. 4-3b). Significant elevations in N concentration were found after one year only with enhancements of 17 and 20% over control for AN and urea respectively.

Whole Plots

The multivariate profile trend in the fertilizer by date interaction was quartic (P=0.044) suggesting a bimodal response. Maximum increments over control occurred at 28 weeks for AN and 52 weeks for urea (Fig. 4-3c). Both fertilizer treatments showed an enhancement over control in current foliage N concentration at 104 weeks after application (Table 4-4). The above differences are in agreement with those in the inner plots but their magnitudes are generally reduced (Table 4-4).

One-year-old needles from whole plots showed significant increases in foliar N concentrations only at one year after application (Fig. 4-3d). Increments over control were diminished from inner plot values to 15 and 17% for AN and urea respectively.

Effects Within Crown Class

As for the whole plots, peak concentrations in foliar N within crown classes were observed 28 and 52 weeks after fertilization for AN and urea respectively (data not shown). Differences between fertilizers occurred in the behaviour of foliar N within crown classes on a given date, however. Dominant and codominant trees achieved higher foliar N enhancements than intermediate trees under AN treatment (Table 4-4). Conversely, urea always elevated foliar N concentrations of intermediate trees farther over control than was the case for dominant and codominant trees. Two years after application of AN significant elevations in foliar N concentration remained for dominant/codominant trees but not for

Table 4-4. Increment over control (%) in N concentrations of current foliage after fall application of N @ 200 kg ha^{-1} as AN or urea.

		Weeks after application							
		28		52		78		104	
Trees included	Source	(May 30/83)		(Nov 26/83)		(May 25/84)		(Nov 26/84)	
WHOLE PLOT	AN	20.1*	0.060*	14.0	0.043	-	-	8.8	0.100
	Urea	-1.6	0.856	15.2	0.032	5.6	0.340	8.3	0.113
Dom/Codom	AN	22.7	0.079	14.9	0.032	-	-	12.4	0.033
	Urea	-1.6	0.888	10.9	0.091	6.7	0.339	7.5	0.146
Intermediate	AN	17.2	0.041	12.0	0.158	-	-	5.0	0.465
	Urea	0.5	0.935	22.6	0.023	7.6	0.154	12.1	0.103
INNER PLOT	AN	25.3	0.027	16.7	0.054	-	-	7.9	0.151
	Urea	0.3	0.967	19.4	0.030	6.4	0.387	9.5	0.094
Dom/Codom	AN	30.2	0.034	17.7	0.050	-	-	12.3	0.075
	Urea	0.1	0.991	13.5	0.113	9.0	0.325	8.4	0.194
Intermediate	AN	21.9	0.042	14.5	0.138	-	-	5.4	0.286
	Urea	7.1	0.433	27.9	0.017	10.2	0.057	16.4	0.012

* Data pairs under a date are %increment, followed by probability of making a Type I error when difference from control is declared.

intermediate/suppressed (Table 4-4). For urea, significant elevations remained after two years for intermediate/supressed trees but not for dominant/codominants (Table 4-4). These differences were not connected to any systematic feature in the lateral distribution of trees in various crown classes within plots. Tree height did not correlate with distance from center of any plot (results not shown).

In the spring following fertilization a marked discrepancy was observed in the partitioning of N between juvenile and one-year-old needles in the urea treatment (Fig. 4-4). Mature foliage at that time had slightly higher N concentrations in control than in urea-fertilized trees. Conversely, a much higher N concentration was observed in juvenile needles under urea fertilization. AN-fertilized trees had similar N enhancements in both year classes of foliage. By the fall following fertilization N increments were similar in current and one-year-old needles of fertilized trees. Some of the impact of nutrient additions may be masked by dilution into larger needles. To overcome this, we examined N levels on a per needle basis also. Results of this procedure are discussed below.

Spring vs Fall

Calculation of N mass/needle of current and one-year-old foliage in the first fall after fertilization reveals clear differences in the various treatment combinations (Fig. 4-5). Taking AN and urea treatments together at this stage, needle N masses were increased over control by 9 and 30% for one-year-old and current ages respectively (Table 4-5, $P<0.001$). Combining seasons of application, needle N mass averaged 26% over control in AN treatments; while urea treatments were associated with a 13% increase ($P=0.100$). Spring and fall applications resulted in mean increases in needle N mass over control of 17% and 23%, respectively. Seasons of application were not statistically different ($P= 0.21$).

In the first spring after fertilization AN was more effective ($P=0.076$) at raising N mass per needle than was urea, irrespective of season of application (Table 4-5). Fall application

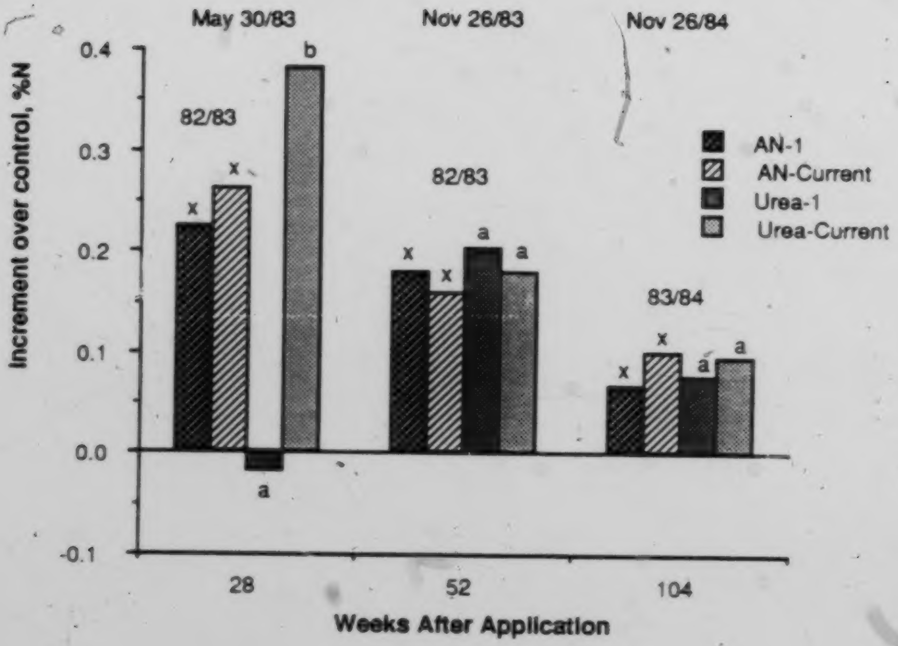

Figure 4-4. Enhancement of nitrogen percentage over control in current and one-year-old foliage at four dates following fall application of AN or urea to Douglas-fir. Lowercase letters indicate differences (P<0.10) within a fertilizer source. Numbers refer to year in which foliage flushed.

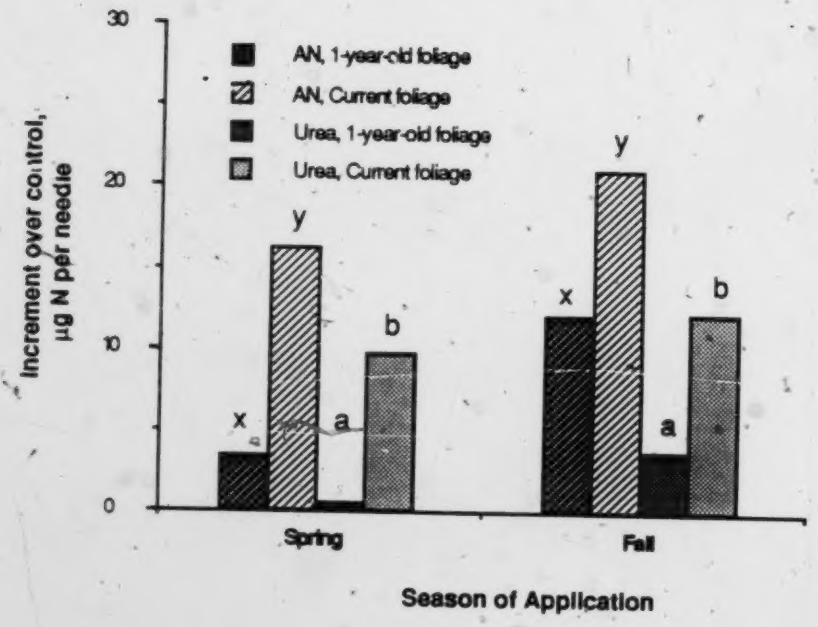

Figure 4-5. Enhancement of N mass of current and one-year-old needles in the fall after application of AN or urea in spring or fall to 38-year-old Douglas-fir. Different lowercase letters indicate statistical differences within a fertilizer source.

Table 4-5. Mean Douglas-fir needle N mass increments (μg needle^{-1}) over control at four dates after spring or fall fertilization with AN or urea. Bracketed data are % increments. Observations are for current foliage except in the first fall after fertilization where both one-year-old (left value) and current foliage were examined.

	Season of Application							
	Spring 1982				Fall 1982			
	Time after Application							
	Year1 (1982-3)		Year2 (1983-4)		Year1 (1983)		Year2 (1984)	
Fertilizer Source	Fall (Dec 17)	Spring (May 30)	Fall (Nov 26)	Spring	Spring (May 30)	Fall (Nov 26)	Spring (May 25)	Fall (Nov 26)
AN	3.3, 16.0	8.3	-	-	12.3	11.9, 21.0	-	15.5
	(6.0, 37.3)	(18.7)			(26.4)	(23.9, 38.5)	-	(26.8)
Urea	0.4, 9.6	4.0	5.4	-	-5.6	3.6, 12.1	6.9	8.7
	(0.7, 22.3)	(8.9)	(11.4)		(-12.0)	(7.2, 22.3)	(15.0)	(15.0)

of urea actually resulted in a small depression of needle N mass in the following spring, an effect also noted with needle N concentration (Fig. 4-4).

In urea treatments N contents of needles formed immediately after fertilization continued to be significantly greater than control in the second fall after fertilization (Table 4-5) but differences between seasons of application were not statistically significant (P=0.32), related to high variation among plots. Two years after fall fertilization, N mass/needle was higher in trees which received AN rather than urea (P=0.08).

4.4 Discussion

The current foliar N concentrations found in fall for control treatments in this study (approximately 1.1%) suggest that productivity on this site is limited by available N (Heilman and Gessel 1963). Therefore, a foliar N response from fertilization was expected. Here significant elevations of foliar concentration and content of N were detected under all combinations of time of application and fertilizer chemical source.

Foliar N concentrations generally were maximal in current foliage in the fall after fertilization. This result is in agreement with other studies on Douglas-fir (Brix 1981a, Heilman et al. 1982, Miller et al. 1986).

Foliar N concentrations of a given cohort were seasonally variable throughout the study, even in control treatments. For example, N concentrations of 1981 foliage in spring control trees at -1 wk (Fig. 4-1a) and 30 wk (Fig. 4-1b) differed by approximately 25%. Because no significant changes in foliar mass were detected this dynamic behaviour must reflect movement of N within the plant. Van den Driessche and Webber (1975) and Margolis and Waring (1986) have provided direct evidence for the existence of a mobile pool of N in Douglas-fir seedlings. Our results confirm that appreciable retranslocations occur also in Douglas-fir at crown closure.

Nambiar and Fife (1987) reported that young radiata pine retranslocates as much as 57% of the N in newly-matured foliage. They noted that periods of rapid retranslocation of

N coincided with production of shoots and speculated that most of this N was directed primarily toward aboveground apical meristems. In the present study periods of shoot emergence and elongation were associated with large variances in foliar N concentrations. Presumably, factors affecting nutrient availability and transport (microsite, genetics, crown class) will accentuate differences in foliar N concentration at times of active retranslocation.

Because variances in foliar N concentrations fluctuated temporally data were analyzed by multivariate ANOVA, which does not require the assumption of compound symmetry (Morrison 1976), followed by planned contrasts. Standard errors for contrasts are constructed only from data derived from the date of interest. As a result a given difference in foliar N concentration could be significant on one date and not another.

Spring Patterns

Brix (1981a) and Miller et al. (1986) noted higher fall concentrations of N in current foliage for spring-applied AN than for urea and this was also the case in the present study although the difference was statistically significant only for the one-year-old needles (Fig. 4-1). It appears that AN raises N availability more in the first few months after application than does urea. Some reduction in urea-N availability occurred on this site as a result of volatilization of ammonia (Chapter 3); however, it is likely that uptake differences related also to differing patterns of N mobility and reactivity also.

By spring of 1983 no significant difference in foliar N concentrations existed between fertilized and control trees (Table 4-3). However, at that time a new flush was emerging which seemed to affect N levels in the older foliage. Differences of approximately 10% in tissue N concentrations were not significant at the end of May but were significant 6 months later (Table 4-3). Two years after fertilization (May 25, 1984), when 10% increments were again significant, swollen vegetative buds were present but none had burst. The earlier phenological stage sampled in spring 1984 may have been responsible for the greater statistical significance attached to enhancements of foliar N concentration similar to those of the previous spring (Table 4-3).

Because initial fertilizer response may include expansion of needles as well as an increase in N concentration (Leaf 1973), the N mass of the needle may be the best indicator of potential growth response (Weetman 1971, Timmer and Stone 1978). The duration of a significant treatment response in this experiment was dependent upon analysis of foliar N as concentration or mass. For example, N concentrations following urea fertilization were not different from control in the spring, and only marginally different in the following fall after fertilization (Table 4-3). However, when the N mass of these same tissues was calculated, there were significant enhancements over control at both stages (Table 4-5).

Whereas spring-applied AN frequently resulted in higher N concentrations in foliage than did urea (Fig. 4-1), the only significant contrast between the two N sources was for one-year-old foliage 6 months after application. When current foliar N data from 6 months after application were expressed as foliar N mass (Fig. 4-5) AN resulted in a 67% greater increment over control. Dangerfield and Brix (1979), working in a stand of lower productivity than the one studied here, reported uptake into current Douglas-fir foliage to be over 100% greater for AN than for urea.

Fall Patterns

Elevated concentrations of N in current foliage were found 6 months after fall fertilization only for AN (Fig. 4-3). From a standpoint of elapsed time only, the fall urea treatment appears anomalous as all other treatment combinations caused maximum rise in foliar N concentration after 6 months. Phenologically, however, the fall AN treatment stands by itself, in that maximum concentration response occurred in the spring and for all other treatments it was in the fall. Whereas urea did not raise current foliage N status in the spring after application there was an appreciable elevation in N concentration of elongating, juvenile shoots (Fig. 4-4). Thus, the failure of urea to elevate N levels in 1982 ("current") foliage was not due to zero uptake of fertilizer N, rather a lower uptake or different allocation than occurred in AN-treated plots. Urea-fertilized trees apparently had acquired sufficient N by spring to enhance levels in emerging shoots but not enough to reduce retranslocation from older needles. By contrast AN-fertilized trees had apparently gained sufficient N to allocate in significant amounts to at least two age classes of foliage.

The initial uptake patterns for urea and AN differed sharply but both N sources produced similar effects on whole-plot foliar N concentrations at one and two years after application (Fig. 4-3). Differences between the N sources arose again, however, in the degree of response observed between crown classes. When fall-applied, urea enhanced the foliar N status of intermediate trees more than dominant/codominant trees on every sampling occasion (Table 4-4). This effect may be related to differences in rooting habit between the two crown classes. In coarse-textured forest soils urea-N has been found to be less mobile than AN-N (Overrein 1969, Pang and McCullough 1982). Accordingly, plants rooted at shallower depths may have an advantage over deeper-rooted individuals when acquiring urea-N. Shallower rooting by intermediate trees may be an adaptative mechanism to gain advantage in access to nutrients mineralized during decomposition of fresh residues. Helms (1965) has described compensatory photosynthetic efficiency at the needle level for suppressed trees. It seems likely that other adaptive strategies would exist for intermediate and suppressed trees. Barclay and Brix (1985) reported greater proportional diameter and volume growth of Douglas-fir among smaller diameter classes in response to urea fertilization.

Two years after fall fertilization foliar concentrations of fertilized trees were about 9% greater than the control (Table 4-4). Miller et al. (1986) reported a similar magnitude of enhancement at the same stage when AN and urea were fall-applied at 224 kg N ha^{-1}. Heilman et al. (1982) reported no difference from control in N concentrations two years after urea fertilization of young Douglas-fir at 224 kg N ha^{-1}. The study of Heilman et al.

(1982) was carried out on high fertility silt loam soils whereas the present study and that of Miller et al. (1986) were conducted on coarse-textured, medium-productivity soils derived from glacial till and glacio-fluvial materials. The probability of a growth response to N by Douglas-fir is inversely related to site quality (Edmonds and Hsiang 1987). Perhaps a corresponding relationship applies to the duration of a treatment response.

Spring versus Fall

The overall effects of spring and fall applications of urea and AN are best illustrated in Fig. 4-5. Apart from the obvious enrichment of current over one-year-old foliage two features emerge: 1) AN caused greater elevations in foliar N content than urea and 2) this early superiority was not conditional upon application in one particular season. In fact, the maximum uptake of N to foliage occurred under fall application of AN.

Miller et al. (1986) noted a significant interaction between source and season for a study involving urea and AN applications to 29-year-old Douglas-fir. They reported maximum fertilizer efficiency for AN when spring-applied and; for urea, when fall applied. Their observations are in agreement with predictions made by Ballard (1984) for the optimum application conditions for these two sources. Overrein (1969), Pang and McCullough (1982) and many others have documented the potential for leaching losses of nitrate from forest soil. Generally, leaching is predicted to be accentuated under conditions of high rainfall, low evapotranspiration, high nitrate concentrations and low root activity.

The high efficiency of AN in fall application was not expected. The soil was well-charged with moisture at the time of fertilization and rainfall in the following week was intense, totalling over 10 cm (Chapter 3). Requisite conditions for leaching appear to have been present after fall fertilization, yet, maximum fertilizer uptake into foliage was obtained for AN in this season of application. It is not possible from the present data to say with certainty why this result was obtained. However, it seems likely that substantial uptake of nitrate in late fall and possibly, through winter, was involved. If nitrogen uptake were solely from ammonium sources the fall-applied urea should have provided optimum N availability because volatilization was negligible, ureolysis was rapid and fertilizer N was favourably distributed throughout the soil profile (Nason et al. 1988). Margolis and Waring (1986) have shown substantial uptake of N from AN in Douglas-fir over-wintered in a nursery seedbed. In the present experiment leaching of nitrate by fall and winter rainfalls did not negatively affect fertilizer efficiency.

Douglas-fir seedlings have been shown to efficiently take up nitrate from sand culture (Van den Driessche 1978) and stirred nutrient solutions (Rygiewicz et al. 1984). Krajina et al. (1973) have proposed that this form of N is a major source for Douglas-fir in the field; yet, many soils, including the one in this study, supporting growth of this species contain no appreciable nitrate and fail to accumulate nitrate upon aerobic incubation in the laboratory. The role of nitrate and nitrification in the nutrition of Douglas-fir forests requires additional study.

The ranking of treatment efficiencies suggested by Fig. 4-5 and Table 4-5 viz. fall AN > spring AN ≈ fall urea > spring urea is consistent with the concept of a highly efficient root system limited in N acquisition by spatial and diffusional properties of the soil. Rainfall accompanying fall fertilizer applications apparently promoted contact between fertilizer N and the tree root system. Spring fertilization, followed by an extended dry period (Chapter 3) was less effective within a fertilizer source. It is likely that both biological (e.g. mineralization-immobilization relationships) and physico-chemical mechanisms were involved in moderating the responses reported.

4.5 Conclusions

Intermediate productivity Douglas-fir at crown closure were found to respond to N-fertilization by increasing: the N concentration of existing foliage and both the concentration and content of N in foliage emerging from vegetative buds already set. As described for seedlings and saplings, foliar N was dynamic within and between years and greatest increases occurred in youngest needle cohorts.

Differences were found in the degree of response as influenced by chemical source and season for application of fertilizer N. The hypothesis that urea-N fertilizer would be taken up in greater amounts in fall was supported. Part of the lower uptake of urea-N in spring was attributable to volatile loss but differences in availability and reactivity probably contributed as well. The hypothesis that AN would be better suited to spring application was not supported in spite of the occurrence of requisite weather conditions for a rigorous test. Fall application of AN raised foliar N status more than did urea in the same season. The greater availability of AN-N to Douglas-fir was inferred to be due to the direct uptake of nitrate.

4.6 References

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5. DYNAMICS OF FOLIAR N IN DOUGLAS-FIR. II. UPTAKE AND TURNOVER OF N AFTER SPRING AND FALL APPLICATION OF ^{15}N UREA

5.1 Introduction

Recent abatements in the supply of coastal timber have rekindled interest in intensive silviculture. Growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco), in B.C. and the Pacific Northwest of the U.S. has been shown to be limited by N in many fertilizer trials (e.g., Heilman and Gessel 1963, Miller and Harrington 1979, Barclay and Brix 1984). Favourable economic growth responses are common but a good deal of imprecision exists in growth response predictions at the stand level. The utility of forest N fertilization to the manager could be greatly enhanced by even a modest increase in response prediction accuracy.

Factors limiting the accuracy of response prediction include lack of accurate estimates of rates and amounts of N taken up after fertilization and the long term fate of both the residual fertilizer N and that incorporated into trees. Estimates of Douglas-fir N uptake ranging from less than 20 (Turner 1982) to over 100 kg ha^{-1} (Cole 1981) have been reported. Part of this variation has been attributed to stand and site factors, but errors inherent to the allometric equations used to compute masses of dry matter and nutrients are compounded when differences are taken. Additionally, complex internal redistribution patterns exist in the tree which make timing of tissue sampling important.

It has long been recognized that N in leaves of trees is dynamic. Northern temperate conifers frequently have cycles in the concentrations of N in a given cohort of foliage. The normal pattern reported for mature foliage of coastal Douglas-fir (Smith et al. 1981, Heilman et al. 1982, Chapter 4) is modal and involves an increase from a minimum coincident with budbreak in mid-spring to a maximum occurring in late fall to mid-winter.

Occasionally, a secondary trough is seen in early to mid-fall. These fluctuations have been interpreted as representing transfers of N among tissues of varying N demand. For example, the decline in N concentration of mature foliage preceding the spring emergence of new shoots has been suggested to reflect movement of N directly to new shoots from older needle cohorts. Examination of shoots or xylem sap from a variety of conifers (van den Driessche and Webber 1975, Margolis and Waring 1986, Pietiläinen and Lähdesmäki 1986, Kim and Glerum 1988) have shown wide seasonal fluctuations in both the absolute and relative amounts of various ninhydrin-reactive compounds. Generally, the N-rich amino acids arginine and glutamine comprise the greatest part of the mobile N pool. The complexity of N uptake and retranslocation in trees has lead to the need for simulation models to simplify, organize, and test knowledge.

Advanced models have appeared recently that relate nitrogen nutrition to growth performance of conifers (Ågren 1985, Ingestad 1988). The central features of these models are that first, dry matter production is expressed through the relative growth rate and this is a function of total N in the canopy. Second, N uptake is regulated by the N flux density, or ability of the soil to provide mineral N to the roots. Hence, growth in a given year is a reflection of the accumulation of N over at least one, if not several, previous years; but consumption of N during growth draws down reserves and ultimately, ties growth to the availability of N in soil. These models appear to integrate well the fundamentals of tree nutrition but cannot shed any light on internal retranslocation or feedback between N status and quality of litter added to the soil system because biomass is treated as a single pool.

Fagerström and Lohm (1977) proposed that growth in Scots pine could be described as a function of the mass of foliage, and that this was set by the magnitude of a mobile pool of N within needles. Nitrogen in needles was either structurally-bound and therefore, static, or mobile. Production of needles in a given year was a function of biological potential, set by the the previous season's nutritional history, and the growing conditions of the current year. An important aspect of their treatment is that N for a new foliar cohort is derived directly from older foliar cohorts. Their model described available data for Scots pine quite well in a qualitative sense but contained parameters whose biological significance remains unclear. The models of Ågren (1985) and Ingestad (1988) have formalized the concepts of Fagerström and Lohm (1977) in a set of differential equations linking internal cycling to a soil N supply submodel. These models have not apparently been fully parameterized or validated, however.

Use of tracer nitrogen (^{15}N) offers several potential advantages as an alternative to a straight mass balance approach to uptake. First, its use allows estimation of process rates when the state variables of interest show little or no amplitude. Second, the fate of the applied N may be followed quantitatively. Finally, a fairly complete description of the system in some cases can be built in the form of a simulation model. A model ultimately helps in the understanding and exploitation of a natural system but probably makes its greatest contribution to knowledge in the way it fails to fully describe system behaviour. Model deficiencies frequently provide clues as to what critical understanding is lacking.

A small number of tracer N studies have been carried out on coniferous trees (Nômmik 1966, Mead and Pritchett 1975, Heilman et al. 1982, Melin et al. 1983, Pang 1985, Nambiar and Bowen 1986, Melin and Nômmik 1988). While providing useful information on the qualitative, and sometimes, quantitative fate of applied N, little kinetic analysis has been presented with the exception of Nambiar and Bowen (1986). A further shortcoming of these studies is that they were conducted on very small trees, or on somewhat larger trees which were root-isolated. Thus no tracer work has been reported for a typical Douglas-fir candidate stand for fertilization: i.e. a moderately stocked, medium to upper medium productivity stand approaching crown closure and showing indications of N deficiency.

The present study was undertaken to examine the dynamics of fertilizer N in a medium productivity stand as affected by season of application of urea fertilizer. We hypothesized that the balance in N availability to microbes and plant roots might be shifted in favour of plant uptake when urea was fall-applied because lower temperatures and higher rainfall would first, serve to retard organic matter extraction accompanying ureolysis (Foster et al. 1985) with attendant microbial immobilization (Salonius 1972), and second, promote redistribution of N throughout the rooting zone. In addition, information on the long-term fate of N was sought. Currently, disagreement exists on the effect added N has on the internal economy of N in the plant. Some researchers have interpreted N cycling rates to be positively related to nutrient stress (Turner 1977 , Cole 1981) whereas recent papers (Margolis and Waring 1986, Nambiar and Fife 1987) have proposed that rates of cycling are correlated positively with N availability.

5.2 Materials and Methods

The study site and experimental design are described in Chapter 2. Work discussed in this chapter does not include the AN treatments.

Sample Collection

A detailed description of the procedures and timetable used for foliar sampling can be found in the Chapter 4. Briefly, samples of current and one-year-old foliage were obtained from mid-crown positions of each tree on several occasions over a two and a half year period. On selected dates individual needle masses were determined. Needles were dried at 65 °C and ground (<1 mm) prior to analysis. One additional sampling date was included for the present study. On August 26, 1985 three dominant or codominant trees in each plot of the fall urea treatment were intensely sampled for the purposes of computing aboveground fertilizer recovery. Results of this work are presented in Chapter 7; however, mid-crown foliar N data are utilized here also.

Soils were sampled to a depth of 30 cm using an impact corer (Jurgensen et al. 1972) of 57 mm inner diameter, at nine grid locations established by orthogonal trisection of each plot. Samples were composited within plot by horizon (forest floor) or by 10 cm depth increment (mineral soil).

Laboratory Procedures

Forest floor samples were air-dried and ground to pass a 2 mm sieve in a Wiley mill. Mineral soils were air-dried and passed through a 2 mm sieve prior to analysis. Ammonium in soil samples was extracted with 2M KCl (Keeney and Nelson 1982) using 5:1 or 10:1 solution to soil ratios for mineral soils and forest floors, respectively. Isotope ratios were determined as described below.

Samples of ground foliage were digested using a modification of the sulfuric acid/peroxide method of Thomas et al. (1967). Ammonium in the digests was determined on an AutoAnalyzer (Technicon Industrial Systems 1977). Ammonium in subsamples of the digests was recovered for mass spectrometry by steam distillation into dilute boric acid. Titrated distillates were acidified with H_2SO_4 and dried at 55 °C in preparation for mass spectrometry. Ammonium sulfate salts were oxidized with LiOBr (Porter and O'Deen 1977) and the 29/28 ratios of the resultant dinitrogen determined in a Micromass 602C dual inlet stable isotope ratio mass spectrometer.

Data Analysis

Nitrogen contents of needles were calculated for plots by summing for individual trees the product of needle mass and N concentration over all trees in the stand. After current foliage had reached maturity in fall it was assumed for the purpose of calculating N content of needles that the unit weight did not change over the following 18 months (Smith et al. 1981). The proportion of N due to fertilizer (PDF) in a foliar sample was calculated as the quotient of ^{15}N excess in the tissue and fertilizer source. Percent fertilizer N in foliage was calculated in a similar manner to N content - the product of N concentration and proportion due to fertilizer were computed at the tree level. Orthogonal contrasts were used to indicate differences between seasons of application on selected dates. Unless otherwise stated differences are declared at the level of P=0.1.

Foliage mass was calculated using regressions on breast height diameter prepared by Grier et al. (1984). These regressions, which treat fertilized and control trees separately, are based on data from Washington state Douglas-fir in the same productivity class (site class III) as those in the present study. Additional similarities in the study of Grier et al. (1984) and the present study include soil parent materials, understory vegetation, chemical source and rate of N fertilization, and stocking level (1000 stems ha^{-1}). This aggregate of similarities was the basis for selecting these regressions over other available sets. During the first year after fertilization the mass of current foliage was calculated from regressions for control trees but adjusted for any measured increment over control in unit needle mass. The mass of the second cohort of needles to appear after fertilization was computed using the regression for fertilized trees in Grier et al. (1984). The allometric regressions used for aboveground biomass (Grier et al. 1984) were generated from trees that had completed the annual litterfall cycle. With the exception of July 20/82 and May 30/83 the study trees were in phenological conditions that matched, from a standpoint of the suite of foliar cohorts present, those trees used by Grier et al. (1984). Foliage mass on July 20/82 was equal to that predicted by the regression plus the mass of the new flush. Trees sampled on May 30/83 were assumed, on the basis of visual estimates, to have 25% of the mass of the 1983 cohort in addition to the foliage mass predicted from regression. All mass computations relying on logarithmic regressions were adjusted for bias as suggested by Baskerville (1972).

Compartmental Analysis

Compartmental analysis as a tool for ecosystem analysis has been most useful under steady state assumptions. However, the general theory of simultaneous differential equations underlying compartmental analysis can be applied in non-steady-state systems as well (Jacquez 1972). The resulting systems of equations are often nonlinear and difficult, if not impossible, to integrate by analytical methods. Iterative nonlinear estimation methods now available have the potential to expand the utility of compartmental analysis to include certain non-steady-state conditions. Here we calculate uptake of fertilizer N to one-year-old foliage from estimated parameters in a simple system of differential equations describing the decline in specific activity in soil ammonium and the concomitant rise in one-year-old foliage of trees:

$$\frac{dA_1}{dt} = -k_1 A_1 \qquad [1]$$

$$\frac{dA_2}{dt} = k_2(A_1 - A_2) \qquad [2]$$

where

A_1 is the proportion due to fertilizer (PDF) of the soil ammonium pool

k_1 is the first order rate coefficient, wk^{-1}

A_2 is the lagged PDF of one-year-old foliage

k_2 is the turnover rate of N in one-year-old foliage, wk^{-1}

The system of equations above is derived in Appendix 1. Equation [2] arises directly from the mass balance for the tracer when the size of the second compartment is assumed constant (Nishio et al. 1985, Myrold and Tiedje 1986). This assumption was felt to be adequately met for one-year-old foliage, but not current foliage, during the first 6 months after fertilizer application because there was little, if any, change in needle mass and N concentration rose by an average of only 0.2% (Chapter 4). Data from only the first 6 months is used because after this time it was felt that N sources internal to the tree may become important in supplying this cohort. The ^{15}N excess in soil ammonium was computed as an average weighted by the mass of ammonium within each sampling layer. The procedure assumed all soil ammonium to be equally available to trees, irrespective of depth. Although fine roots were concentrated in the forest floor and first 15 cm of mineral soil the assumption of equal availability was reasonable because little fertilizer N was found below 20 cm (Chapter 6). Tracer data from crowns was lagged by 3 weeks, the amount of time estimated for ^{15}N to appear in the foliage of most study trees. The use of time-lagged data for compartmental analysis is common in pharmacokinetics (Wagner 1975). The procedure permits estimates of turnover without estimating parameters of a compartment that intervenes between the two of interest. In this case the intervening compartment would comprise the root and xylem tissues. Parameters in equations 1 and 2 were estimated using PCNONLIN (Statistical Consultants Inc. 1985), which employed a modified Gauss-Newton iterative algorithm.

We were interested in comparisons between seasons of fertilizer application for the nonlinear uptake estimates above. Inference testing of parameter estimates from nonlinear models is not yet standardized because error distributions associated with the parameters are not well characterized (Weisberg 1985). Maximum likelihood estimation has been found to have a broad utility (McCullagh and Nelder 1983) and is used here. Data for both seasons of application were described using two systems of equations. The first estimated k_1 and k_2 as season-specific for a total of 4 parameters. Second, the system was re-estimated using a common estimate for k_2 - giving a total of 3 parameters. The models were compared by a likelihood ratio test (LRT) (Weisberg 1985) analogous to an extra sum of squares F-test:

$$\mathrm{LRT} = -n\left(\ln\left(\frac{\mathrm{RSS\ (full\ model)}}{\mathrm{RSS\ (reduced\ model)}}\right)\right) \qquad [3]$$

where

n is the total number of observations

RSS is the residual sum of squares

The test statistic is evaluated against χ^2 with degrees of freedom corresponding to the difference in number of parameters estimated in the two models.

An approximate uptake for discrete intervals was calculated to check estimates of uptake obtained from the method described above. A solution of the system represented by [1] and [2] that was used assumes the PDF of the soil ammonium pool to be constant (Sheppard 1962):

$$k_2 = \frac{1}{t} \ln \left(\frac{(A_1 - A_2)_0}{(A_1 - A_2)_t} \right) \qquad [4]$$

where

t is time in weeks, and subscripts on the differences in the numerator and denominator refer to initial and final conditions, respectively.

The condition of constant A_1 was not met in this work. Over sampling intervals it was assumed that A_1 could be approximated by the mean value predicted from the first order rate expression (equation [1]) for each season of application. Estimates of turnover during a period of declining ^{15}N abundance in 1983 foliage were obtained in the same fashion. During this latter stage the source of N was again assumed to be soil ammonium, the specific activity of which was calculated by linear interpolation. Generally, *fluxes* of N were calculated as the product of the turnover rate and size of a given compartment.

Fertilizer uptake was calculated by two methods. The first method, "difference method", computed: 1) uptake in both control and fertilized trees from increments and standing stocks of N over time; then 2) *fertilizer* uptake was computed from the difference, between treatments, in these increments. The second method, "static ^{15}N", estimated fertilizer uptake as the product of the mass and proportion due to fertilizer of N in foliage

Finally, total uptake of N in fertilized plots was calculated as the product of the turnover rate (k_2) and the mass of N in older foliage *plus* any fertilizer N increment in new needles.

5.3 Results

Edge effects are a well-known source of error in fertilizer plot experiments. It was thought particularly important to check for this where isotope data would be used for estimates of uptake and turnover. Trees were grouped into four zones of equal area within plots: a central circle, two concentric rings about the circle, and the remaining irregular area to the plot edge. The radial distance to the bisection circle of each zone is plotted against N properties of trees in each zone in Figure 5-1. Nitrogen concentration in current foliage is relatively insensitive to tree position within plot but a distinct decline in isotope enrichment occurs towards the plot boundary (Fig. 5-1). Pooling data on trees located within 5 m of plot center resulted in mean N concentration and ^{15}N excess of 1.27 and 0.822% ,respectively. Thus the depression in the mean values seen at a distance of 5 m in Figure 5-1 is due to the influence of trees in the 5 m class with radii beyond 5 m. Therefore, as in the companion paper (Chapter 4), this radial distance was chosen as a boundary for defining inner plots. Unless specified otherwise, in the remainder of the paper results pertain to observations made on trees in these inner plots only.

Detection of ^{15}N

Jansson (1971) gives the practical lower limit for detection of tracer N as 0.001 atom% excess. In this experiment the spread of observations around a mean of zero suggested that a detection limit of 0.002 atom% excess would be more reasonable (Figs 5-2a&b). On this basis, analytically-significant accumulations of tracer N were detected in a few trees in the first samplings after fertilization. Sampling 2 weeks after spring fertilization found 8 of 42 trees that already contained tracer N atoms in the current foliage (Figure 5-2a). Similarly, samples taken from four trees 3 weeks after fall fertilization had measurable quantities of ^{15}N (Figure 5-2b). In both seasons of application

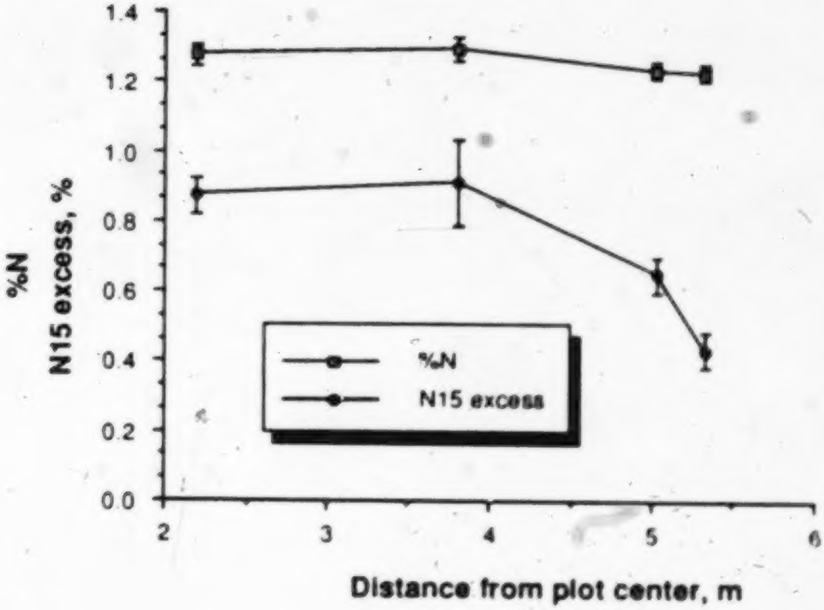


Figure 5-1. Effect of distance of bole from plot center on concentration of nitrogen and ^{15}N excess in current foliage of Douglas-fir one year (spring application) or six months (fall application) after fertilization with ^{15}N-labelled urea. One arm of an error bar indicates the standard deviation for approximately 21 trees.

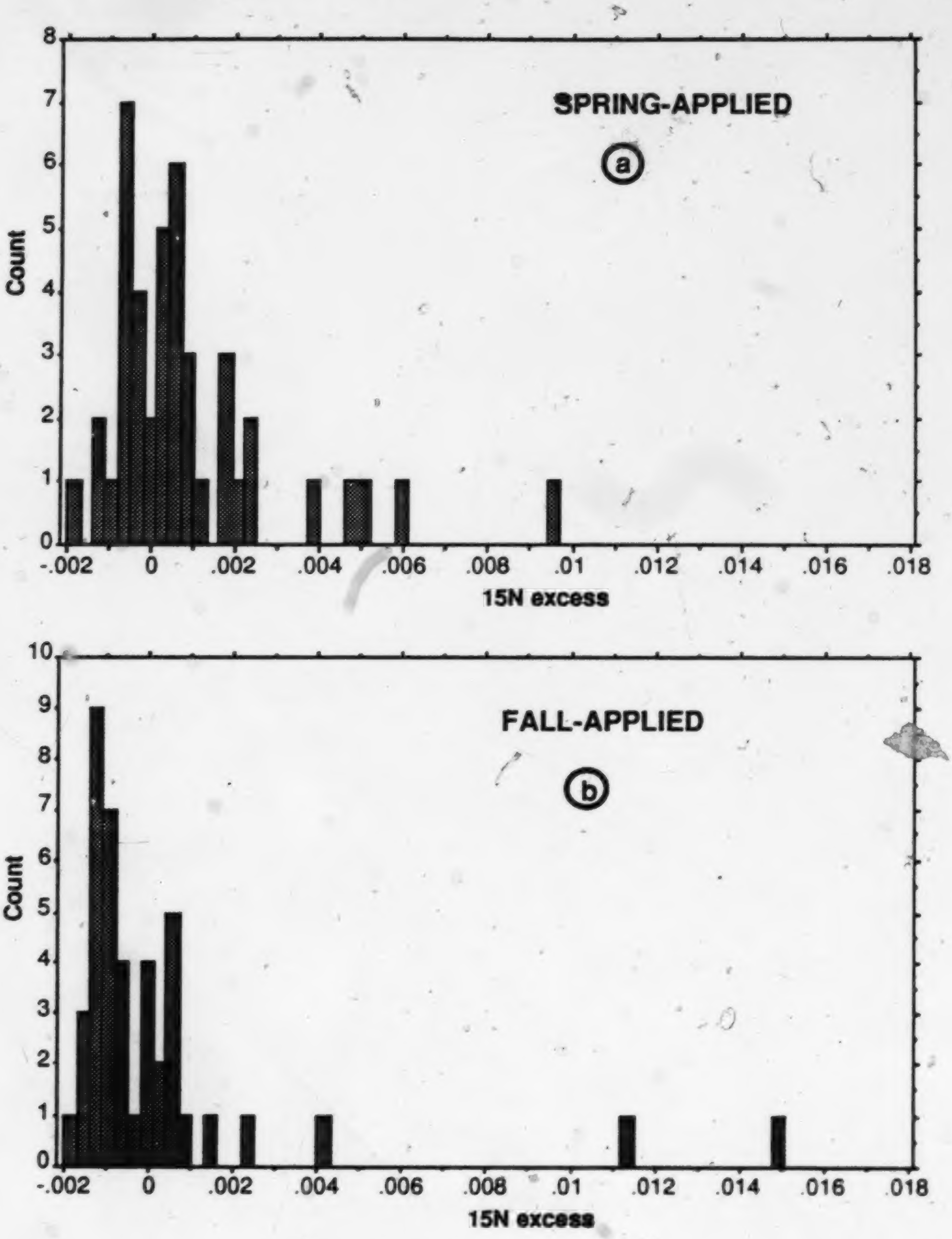
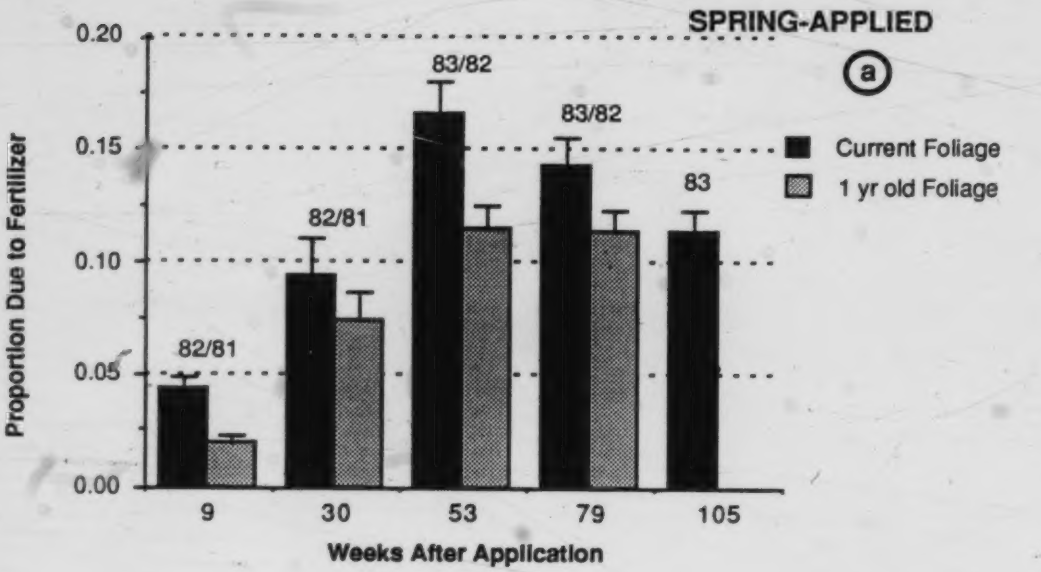


Figure 5-2. Frequency distribution of ^{15}N excess in current foliage of Douglas-fir 2 weeks (spring-application) and 3 weeks (fall application) after fertilization with ^{15}N-enriched urea.

these trees seemed to form a separate population from the majority of trees which showed no significant difference from background levels of ^{15}N. No statistically-significant differences in mensurational characteristics could be found that accounted for trees showing early uptake after spring fertilization. Trees showing early uptake after fall fertilization were, however, shorter than the treatment mean ($P<0.01$ by unpaired t-test). It is possible that this bias to smaller trees reflects primarily shorter path lengths in the xylem. Although more trees surpassed the analytical minimum in the first sampling after spring fertilization, the mean ^{15}N enrichment of fall-fertilized trees was about double that recorded in spring (Figure 5-2a&b).

Spring Uptake Patterns

Whereas only a few trees contained fertilizer N two weeks after fertilization all trees had easily-measured ^{15}N enrichments after nine weeks. At this time approximately 4.5% of the N in needles of foliage formed in 1982 was derived from the urea fertilizer (Fig. 5-3a). This PDF was statistically greater by a paired t-test than that in one-year-old foliage, which averaged 2%. The difference in ^{15}N enrichments in the two ages of foliage is a result of the dilution of incoming labelled N by existing N in the older foliage. The proportion of fertilizer N in foliage of both age classes continued to climb into the fall of 1982. By mid-December, 30 weeks after fertilizer application, 9.4 and 7.4% of foliar N was derived from fertilizer in the current and 1-year-old foliage, respectively (Fig. 5-3a). A substantial flux of N therefore occurred into 1-year-old foliage as well as that maturing in 1982. By spring of 1983, 53 weeks after fertilization, the proportion of fertilizer N had peaked at 11.5% in 1982 foliage. However, juvenile shoots sampled at that time were significantly more enriched in ^{15}N than the 1982 foliage (Fig. 5-3a). The mean proportion of N due to fertilizer in these elongating shoots was very similar to the concurrent weighted mean of the NH_4^+ pool in soil (Fig. 5-4). Prior to this time soil NH_4^+ had always been more highly labelled than foliage.



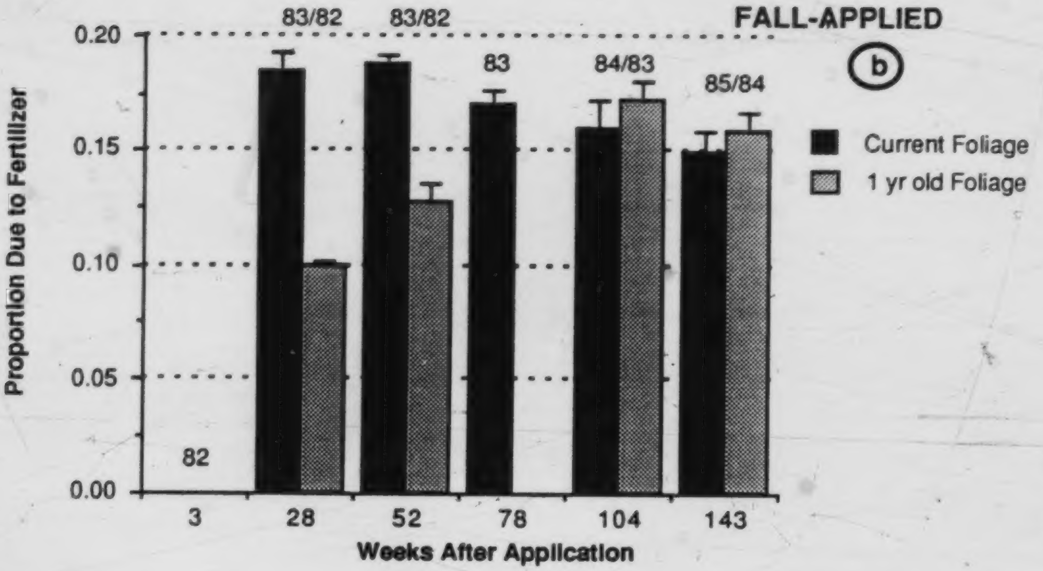


Figure 5-3. Proportion of labelled N in current and one-year-old foliage after fertilization in spring or fall with ^{15}N-enriched urea N@200 kg ha^{-1}. Error bars indicate standard error of the mean.

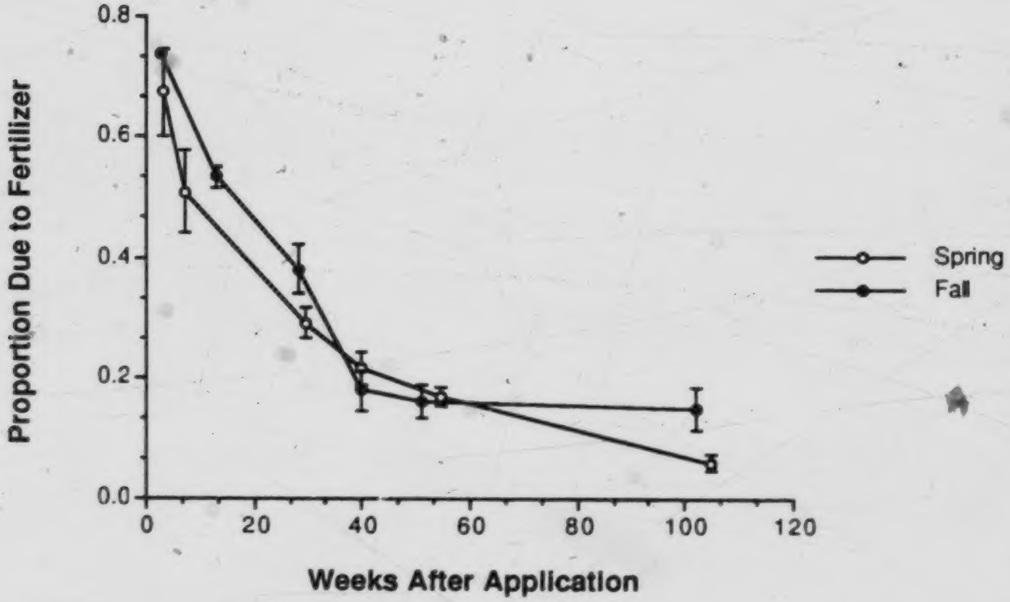
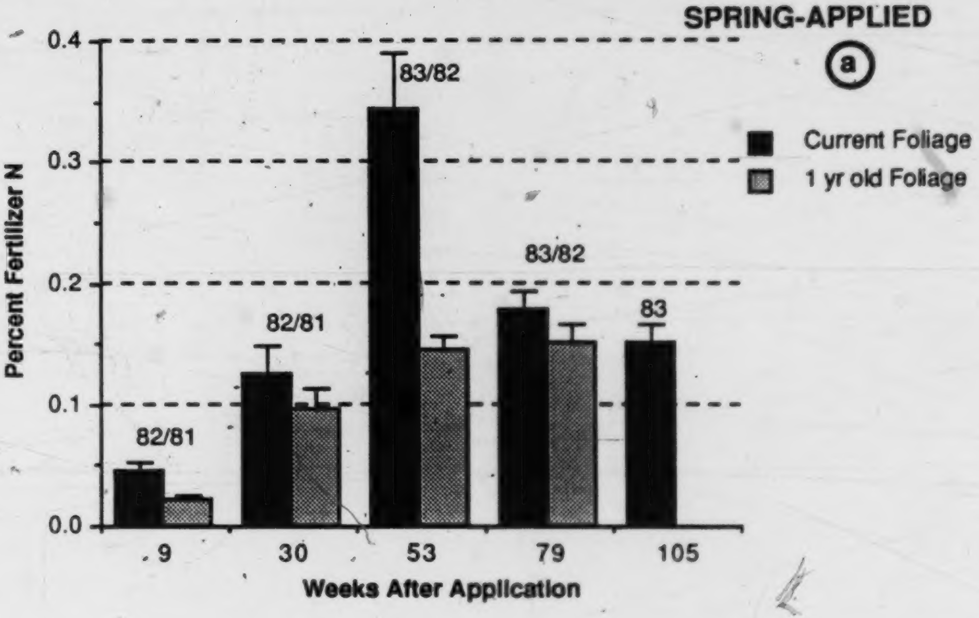


Figure 5-4. Proportion of N due to fertilizer in the ammonium fraction to a depth of 30 cm excluding the LF layer. Proportion due to fertilizer was calculated as the mean weighted by the mass of N in the ammonium fraction of each stratum. One arm of an error bar indicates the standard error of the mean for three plots.

After one year the proportion of fertilizer N in current foliage began to decline but not in one-year-old foliage up to 18 months (Fig. 5-3a). At the end of May 1984, two years after fertilization, vegetative buds had not burst and elongated as they had the previous year. The current foliage examined on this date was thus formed in 1983. This foliage retained approximately 11% fertilizer N.

Total amounts of N in current foliage (Chapter 4) followed a somewhat different pattern to that derived from fertilizer in that maximum concentration, and increment over control, was reached after only 30 weeks. Fertilization thus increased foliar N before availability of *fertilizer* N was maximal. This effect is seen clearly in Fig. 5-5a where concentration of fertilizer N peaks in both foliar cohorts 53 weeks after fertilization. The conspicuous peak for current foliage at this time reflects the very high (>2%) concentrations of N in elongating shoots.

The mass of fertilizer N present in foliage estimated from ^{15}N abundances, N concentrations and the allometric equations of Grier et al. (1984) are shown in Figs. 5-6 and 5-7 for spring and fall applications, respectively. One year after spring application of urea fertilizer, N in foliage reached a maximum of 30 kg ha^{-1}. The estimate of only 20 kg ha^{-1} after 2 years is very likely low because swollen vegetative buds, expected to be highly-enriched in ^{15}N, were present but not analyzed. Additional fertilizer N in other crown structures was not systematically accounted for except in a subset of fall-fertilized trees (Chapter 7); however, occasional measurements on current twigs found ^{15}N enrichments similar to, and N concentrations about 70% of, those in the attached foliage. Based on these figures and stem to twig allometry (Grier et al. 1984) it can be estimated that an additional 2 kg ha^{-1} of fertilizer N resided in these tissues. One-year fertilizer efficiency for the spring application is thus approximately 16% based on leaves and current twigs alone.



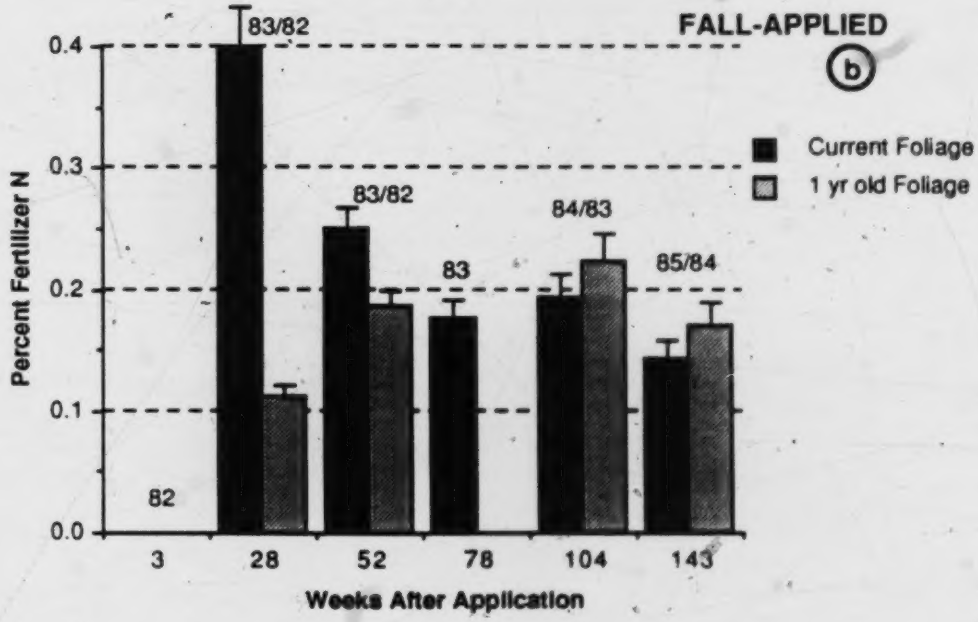


Figure 5-5. Percentage of fertilizer N in current and one-year-old foliage after fertilization in spring or fall with ^{15}N-enriched urea-N@200 kg ha^{-1}. Error bars indicate standard error of the mean.

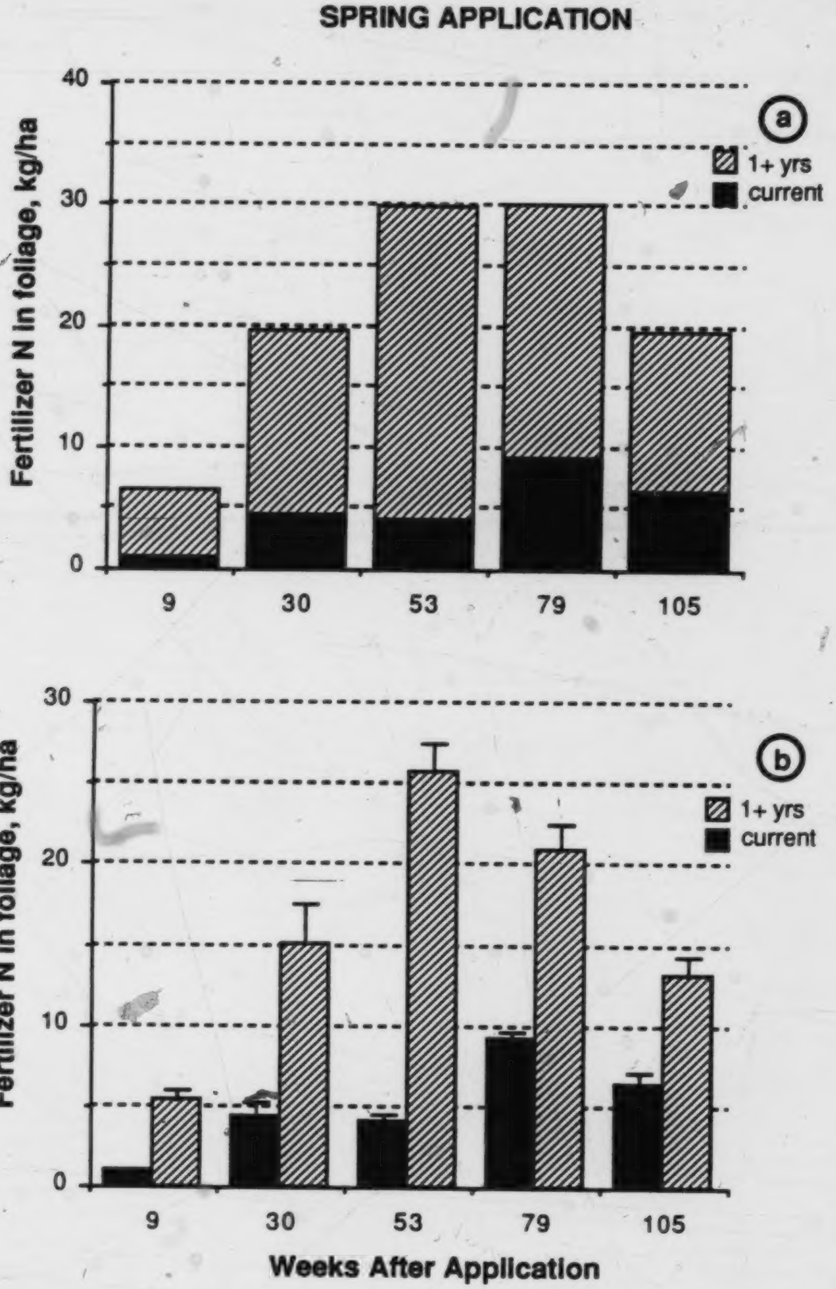


Figure 5-6. Mass of fertilizer N in current and older foliage of Douglas-fir after spring application of urea-N @ 200 kg ha^{-1}. Error bars indicate the standard error of the mean for three plots.

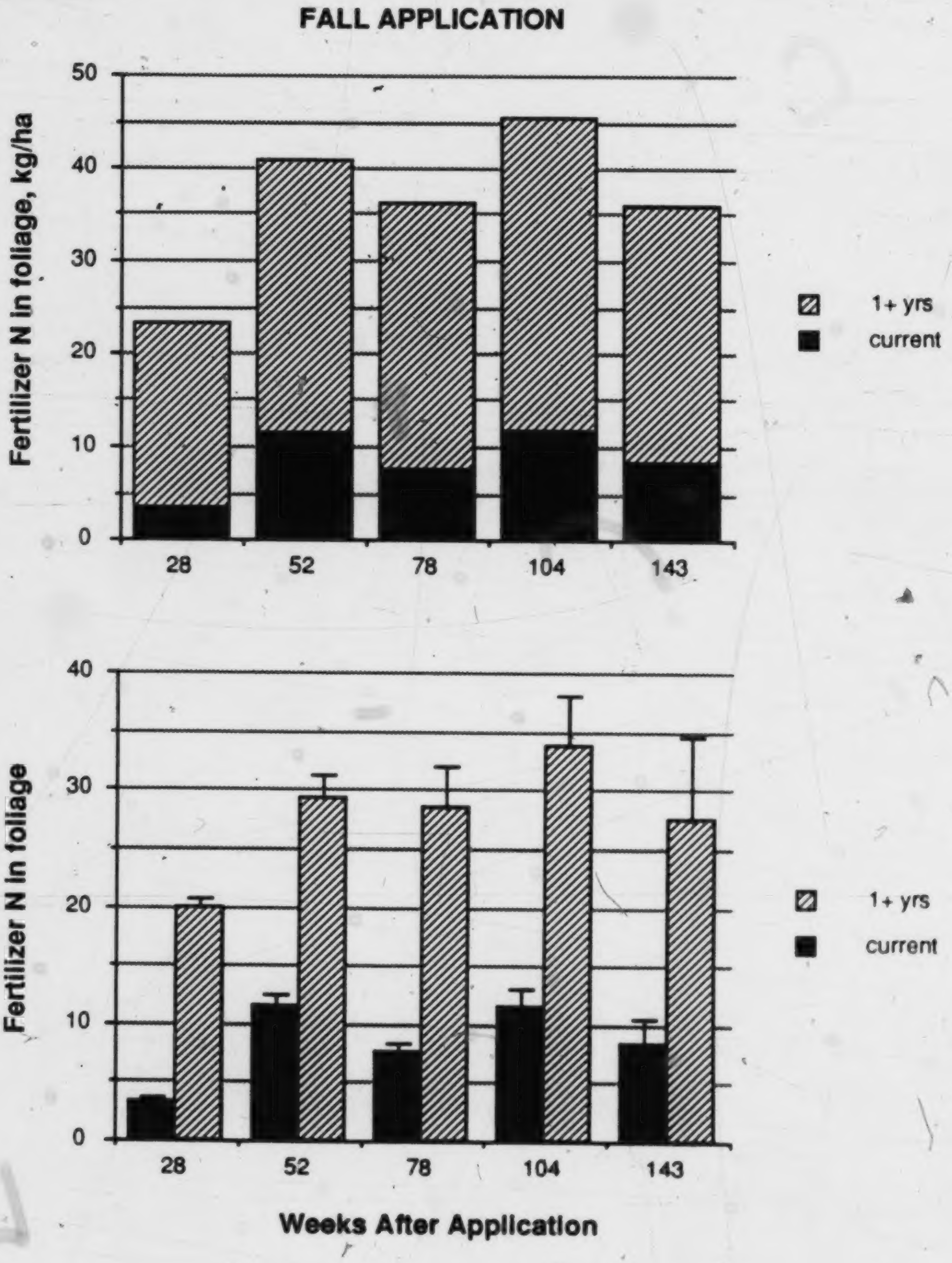


Figure 5-7. Mass of fertilizer N in current and older foliage of Douglas-fir after fall application of urea-N @200 kg ha^{-1}. Error bars indicate the standard error of the mean for three plots.

Fall Uptake Patterns

Foliar sampling of fall-fertilized trees could not be carried out between January and May of 1983. Sampling 28 weeks after fertilization (May 30, 1983) showed that very substantial uptake had already occurred. Nitrogen in needles formed in 1982 was approximately 10% fertilizer origin while this percentage was over 18 in emerging shoots (Fig. 5-3b). Again this difference was significant by a paired t-test and reflected the dilution of fertilizer N by native N in established needles.

In fall of 1983, one year after fertilization, ^{15}N enrichment in current foliage had peaked at 18.7%, whereas the fertilizer N in 1982 foliage was 12.7%. The ^{15}N levels in one-year-old foliage continued at high levels out to 143 weeks after fertilization (Fig. 5-3b). This trend for fertilizer N enrichments in older foliage extended across at least 3 cohorts; viz. 1982, 1983 and 1984. Two years after fertilization and beyond, older foliage had somewhat higher levels of ^{15}N enrichment than did current cohorts, suggesting that the source(s) of N for new foliage was (were) declining in ^{15}N abundance. The generally high level of ^{15}N enrichment in foliage 143 weeks after fertilization showed strong retention of N in crowns.

Peaks in current foliage N mass (Chapter 4) and ^{15}N enrichment occurred simultaneously in the first fall following fall fertilization. Thus peak foliar N levels occurred at the same phenological stage, irrespective of season of fertilizer application, whereas maximum levels of *fertilizer* N in foliage depended more on time elapsed from application.

Fertilizer recovery in foliage after fall fertilization was markedly higher (Fig. 5-7). Allowing for 2-3 kg N ha^{-1} in current, unanalyzed twigs we estimate that fertilizer efficiency at one-year was about 23% for needles and current twigs alone. Peak levels of fertilizer N were reached 104 weeks after application when 46 kg ha^{-1} were recovered. The anomalously low recovery at 78 weeks, in spring of 1984, was probably an underestimate for the reasons given above for the spring treatment. On a whole-crown basis fall-fertilized trees continued to gain fertilizer N after 2 years whereas this was declining in spring-fertilized trees (Table 5-1).

Despite the higher N content and ^{15}N enrichment of fall-fertilized trees one year after treatment (Table 5-1) the estimates of total foliar N in May 1984 did not differ between seasons of application (Table 5-2). Total N in crowns on this date was based on 1983 foliage alone because 1984 foliage had not yet flushed. No difference in crown dry matter existed between seasons of application on this date (data not shown) so the decline from 332 to 242 kg N ha^{-1} in fall-fertilized trees represents primarily a decline in the concentration of N in 1983 foliage. This indicates that, despite the greater uptake of fertilizer N by fall-fertilized trees, greater translocation of N from older foliage occurred than in spring-fertilized trees.

Turnover of Foliar N

Estimates of turnover rate based on simultaneous first order equations for proportion of N due to fertilizer in soil ammonium and one-year-old foliage are given in Table 5-3. Despite the rather large standard error in k_2 for spring-fertilized trees a very high proportion of the total sum of squares was explained by the model. The data were better fit by the model in the case of fall fertilization, as indicated by the magnitude of the standard errors for k_2. This reflects the fact that the magnitudes of observations in the soil ammonium pool were greater than for foliage, and minimization of sums of squares is largely accomplished through optimization of the fit for the soil ammonium pool. Nevertheless, a significant reduction in the sum of squares for the data pooled across seasons (indicated by a maximum likelihood estimator compared to Chi-Square) was achieved by use of separate uptake parameters for each season. This procedure is analogous to an extra-sum-of-squares F-test for analysis of covariance in which a rejection of the null hypothesis is evidence for a unique parameter. In this case we interpret the outcome to indicate both a significantly greater (approximately 2X) rate of uptake of soil

Table 5-1. Comparison of foliar N and proportion due to fertilizer at fixed intervals after spring- and fall-application of ^{15}N-urea to Douglas-fir.

	Season of	----------------Weeks After Application-------------			
Property	Application	30 (28)	53 (52)	79 (78)	105 (104) ††
PDF*	Spring	0.074	0.115	0.113	0.123
1-yr-old foliage	Fall	0.093	0.12	0.159	0.161
probability†		0.188	0.712	0.017	0.037
Fertilizer N	Spring	19.8	30.4	30.6	19.9
(kg ha^{-1})	Fall	23.6	41.4	36.7	45.9
probability		0.331	0.025	0.271	0.013
Foliar N Mass	Spring	244	258	255	197
(kg ha-1)	Fall	248	332	242	306
probability		0.695	0.096	0.666	0.035

*PDF: Proportion due to fertilizer

†: Probability of making Type I error when difference between seasons of application is declared

††: Elapsed time after spring and (fall) application of fertilizer

Table 5-2. Comparison of foliar N and ^{15}N enrichment at phenologically-equivalent stages after spring- and fall-application of ^{15}N-urea to Douglas-fir.

Property	Season of Application	Stage After Application 1st Fall	2nd Spring	2nd Fall
PDF*	Spring	0.074	0.115	0.113
(1-yr-old foliage)	Fall	0.12	0.159	0.161
probability†		0.033	0.021	0.018
Fertilizer N	Spring	19.8	30.4	30.6
(kg ha^{-1})	Fall	41.4	36.7	45.9
probability		0.006	0.251	0.066
Foliar N Mass	Spring	244	258	255
(kg ha^{-1})	Fall	332	242	306
probability		0.056	0.644	0.223

*PDF: proportion due to fertilizer

†Probability of making Type I error when difference between seasons of application is declared

Table 5-3. Turnover rate estimates and associated statistics for N in one-year-old foliage of Douglas-fir fertilized in spring and fall with ^{15}N-urea (N@ 200 kg ha^{-1}).

Season of Application	k_1 (SE) wk^{-1}	k_2 (SE) wk^{-1}	Residual Sum of Squares	Total Sum of Squares	Correlation of Needle PDF with Predicted
Spring	0.0288(0.0020)	0.00575* (0.00256)	0.00568	0.18599	0.999
Fall	0.0322(0.0018)	0.01039 (0.00224)	0.00084	0.24728	0.967

* $P<0.025$ by Chi Square statistic using a maximum likelihood ratio test.

NH_4^+ and a faster turnover of this N in the foliage. The coefficients given in Table 5-3 reflect on an annual basis a 30 and 54% turnover in N of spring- and fall-fertilized trees, respectively.

Calculation of turnover using discrete intervals yielded somewhat different estimates (Table 5-4) but confirmed the observation of faster turnover in fall-fertilized trees. Estimations over discrete intervals agreed closely to those from simultaneous equations for spring-fertilized trees but were lower for fall-fertilized trees. It was assumed in the calculations for estimates in Table 5-4 that the source of N for one-year-old needles was soil NH_4^+. Using this assumption for the second year after fertilization produces remarkably high turnover rates. Rates were calculated also assuming a non-labelled source and this resulted in much lower, although still appreciable, estimates (Table 5-4). These latter estimates must be regarded as minimal because there is no other source of N in the plant -soil-system that could dilute foliar N more efficiently. It is even possible that estimates based on a presumed NH_4^+ source are low because there may have been pools of N within the plant that were more highly labelled than soil NH_4^+ after one year.

Turnover estimates from the second year after fertilization appeared to exhibit a reverse trend with respect to season of application in that spring-fertilized trees had higher estimates of annual turnover (46 vs. 19%) based on a natural abundance source (Table 5-4). However, it is more likely that N entering one-year-old needles at this time would be derived from both soil sources and high-turnover internal pools which, by definition, ought to reflect the isotopic abundance of recently-acquired N. Therefore the estimates of approximately 60 to 80% annual turnover, calculated assuming a soil NH_4^+ source (Table 5-4), are more representative of post-fertilization N cycling than the lower estimates based on natural abundance N diluent. This means that N cycling within the tree was accelerated in the second year after fertilizer application.

Transfers of N within the stand were estimated on the basis of total uptake using allometry and foliar N concentrations and contents, and turnover rate estimates (Table 5-5)

Table 5-4. Turnover rate of N in one-year-old needles of Douglas-fir calculated assuming ^{15}N abundance of soil NH_4^+ constant at the mean over stated intervals.

Season of		------Estimated Soil PDF*------			
Application	Period	Initial	Final	Turnover rate	Annual turnover
	wk			wk^{-1}	%
Spring	3-9	0.685	0.577	0.00523	27
	9-30	0.577	0.315	0.00656	34
	79-105	0.077	0.036	0.02879	83
				0.00879	46†
Fall	3-28	0.818	0.365	0.00736	38
	28-52	0.365	0.168	0.00757	39
	52-78	0.168	0.073	0.03216	59
				0.00366	19†

* Proportion due to fertilizer in the soil ammonium fraction to a depth of 30 cm; lagged by three weeks.

† Assumes foliar N diluted by N of natural abundance. Method of calculation otherwise identical to that used for other estimates.

Table 5-5. One-year uptake of N (standard error) by urea-fertilized (N@200 kg ha^{-1}) Douglas-fir estimated by the difference method and by ^{15}N dilution.

		--------Difference Method--------		^{15}N dilution
Season of Application	Estimate, kg ha^{-1}	Control	Fertilized	Fertilized
Spring	Total Uptake*	59.3 (19.3)	100.7(4.8)	56.0 (0.9)
	Fertilizer Uptake	41.4 (4.8)§		30.4 (2.1)
Fall	Total Uptake	21.7 (6.4)	83.0 (6.3)	132.9 (11.9)
	Fertilizer Uptake	61.3 (6.3)§		41.4 (2.3)

* Calculated from difference in mass of N in foliage prior to, and one year after, application of urea fertilizer.

§ Standard error reflects variation among fertilized plots only.

Uptake estimates based on differences in standing stocks of foliar N over time assume that alterations to this pool from internal recycling and litterfall can be cancelled out by making measurements at phenologically-equivalent times. Under this assumption trees fertilized in spring took up 70% more N than control trees, which appeared to take up approximately 59 kg ha^{-1} (Table 5-5). Apparent uptake by control trees for the first year after fall fertilization was less than half this amount but trees receiving urea in fall had nearly as large an increase in foliar N over one year as did spring-fertilized trees (Table 5-5). As a result, the difference estimate of total uptake by fall-fertilized trees was 50% greater than for spring-fertilized trees.

Estimates of fertilizer N uptake by dilution were about 30 and 41 kg ha^{-1} for spring and fall fertilizations respectively (Table 5-5), which are approximately 30% lower than the difference estimates. However, multiplication of the average foliar N mass for the year by the turnover rate estimates for older foliage (Table 5-3) indicates that the flux of N to foliage was 56 and 133 kg ha^{-1} for spring and fall fertilizations, respectively (Table 5-5). Thus, *static* estimates employing ^{15}N were lower than indicated by the mass balance for N, but *dynamic* estimates were much higher in fall and much lower in spring. The smaller spring estimate of N uptake based on turnover calculations is consistent with a fertilizer-enhanced shunt mechanism that raised allocation of native plant N to foliage. On the other hand, the higher flux estimated after fall fertilization suggests recently acquired N was the major source for foliage N, which turned over rapidly.

5.4 Discussion

Uptake

Root-isolated plots for labelled N studies have been deemed necessary to minimize or eliminate lateral movement of fertilizer N and define a rooting area for the study trees (Heilman et al. 1982, Melin et al. 1983). In the few studies that have examined lateral egress of fertilizer N beyond plot boundaries little movement has been recorded. A recent review of environmental impacts of forest fertilization reported that leaching of ammoniacal fertilizers below the root zone has generally been negligible (Nason and Myrold 1989) because immobilization and plant uptake predominate. As to the necessity of root isolation, from the standpoint of in-plot trees, it was found that trees within a 5 m radius formed a homogeneous population with respect to ^{15}N abundance in foliar tissues. This suggests that the rooting systems of these trees experienced the same nitrogen environment. Trees located in plot corners apparently had substantial portions of their rooting volume outside the treatment plots (Fig. 5-1) and these were rejected in the present analysis. It is likely that some of the ^{15}N was taken up by trees outside the plots but it would be expected that this would occur primarily from the rejected edge zone. Total system recoveries were within or above the ranges reported in previous tracer studies (Chapter 7).

Fertilizer N was detected in foliage of some trees after three weeks irrespective of season of application (Fig. 5-2). Heilman et al. (1982) also reported ^{15}N uptake after 3 weeks in 7- and 9-year-old Douglas-fir but these were only approximately 6 m in height whereas trees in the present study were typically 20 m. The bias towards short trees showing earliest uptake under fall fertilization may indicate that transport in the roots, stem and branches is a rate limiting factor in the appearance of labelled N in foliage. Ammonium levels were very high throughout the surface horizons at 3 weeks after fertilizer application (Chapter 6) yet most trees had no ^{15}N enrichment in current foliage. It is clear that a considerable lag occurs between availability of fertilizer N as NH_4^+ and appearance in the needles. These observations could reflect differential rooting patterns among tree size classes but distribution of available forms with depth (Chapter 6) militates against this interpretation. Analysis of xylem sap after fertilization could help resolve the issue.

Estimates of uptake in coniferous forests vary widely with species, stand age, management and method of calculation. This last source of variation is, unfortunately, far from trivial. Calculations may be based on fluxes and changes of standing stocks of soil N (Nadelhoffer et al. 1985) or on direct observations on tree tissues. Usually, the latter method makes use of foliage and/or litterfall only, and uptake is computed as the annual foliar requirement less retranslocation prior to litterfall; with or without adjustment for N immobilized into permanent structures, depending upon whether the system is regarded as being at steady state. Very few studies allow for turnover of N through any component other than foliage. However, recent studies have shown that production of fine roots can exceed that of aboveground net primary production (Persson 1979, Keyes and Grier 1981, Vogt et al. 1981). As metabolically active organs, fine roots represent a significant additional sink for N that is not usually taken into account. Thus, method of calculation alone can be expected to account for large variations in uptake estimates. For example, Ballard and Cole (1974) reported N uptake for 42-year-old Douglas-fir as 20 kg ha^{-1} by aboveground methods whereas Dyck et al. (1987) estimated uptake for 12-year-old radiata pine to be 132 kg ha^{-1} when fine root requirements were included. Direct observations of N requirements by fine roots are not part of the present work but the influence of unmeasured compartments is always exerted in tracer studies and, under certain conditions, can be inferred.

Estimates of uptake here accommodate litterfall inasmuch as the allometric regressions used were generated from trees after fall abscission had taken place. Foliage masses calculated for times between bud break and needle abscission were incremented by the measured or estimated new tissue mass. N uptake was estimated as 59 and 22 kg ha^{-1} in trees used as control for spring and fall fertilizations, respectively (Table 5-5). These values, though variable, bracket the normal range given by Gessel et al. (1973). Variation in the uptake estimates for the control trees in different years underscores the severe pitfalls inherent in assessment of tree N status from observations in a single year. The difference in control uptake estimates stems from the variation in standing stocks of foliar N, which are based on N concentrations and foliar biomass. Control foliar biomass, calculated allometrically from breast height diameter, increased very little over the three seasons of study (data not shown) but foliar N concentrations did (Chapter 4). Foliar N concentrations in the spring of 1982 were very low but rose considerably the following spring - even in the absence of fertilization (Chapter 4). In the present work this is treated as uptake but may represent internal redistribution in response to changing edaphic conditions. This annual variation is, in any case, removed when fertilizer uptake is calculated by the difference method.

Uptake of N in both seasons of application produced significant increases in concentrations, contents and total masses of N in crowns of both spring and fall-fertilized trees (Chapter 4, Tables 5-1, 5-5). The N uptake estimates of 83 to 101 kg ha^{-1} are similar to what was reported after N fertilization of Corsican pine at 168 kg ha^{-1} in three consecutive years (Miller et al. 1976). Uptake by spring-fertilized trees was thus 70% greater than control whereas fall fertilized trees took up 280% more than control.

Difference estimates of fertilizer N uptake were 41 and 61 kg ha^{-1} for spring and fall fertilization, which equate to 20 and 30% efficiency, respectively (Table 5-5). There appear to be very few data in the literature to compare these estimates to, perhaps due to a lack of confidence that allometric regression models generated for unfertilized trees may be used for fertilized trees. Heilman and Gessel (1963) reported uptake of N after N fertilization of Douglas-fir at dosages between 225 and 675 kg ha^{-1} to vary between 33 and 136 kg ha^{-1}. Our first-year uptake estimates are, however, much higher than that reported for 42-year-old Washington State Douglas-fir fertilized at essentially the same dosage (Turner 1977). He reported uptake of only 17 kg ha^{-1} for control and 31 kg ha^{-1} for trees fertilized with N at 220 kg ha^{-1}. On the other hand Miller et al. (1976) recorded approximately 47% efficiency when Corsican pine was fertilized at 168 kg N ha^{-1}. Recovery of N applied at a dosage of 224 kg ha^{-1} was about 26% in slash pine (Mead and Pritchett 1975). Obviously, the proportion of applied N incorporated into foliage over the short term is highly variable and our results do not appear out of line with the range reported for other sites and species.

Tracer N was used to calculate uptake in two alternative ways (Table 5-5). The first, "static ^{15}N method", calculated fertilizer uptake as the product of N mass and PDF in foliage at one year after fertilization and gave estimates of 30 and 41 kg ha^{-1} for spring and fall fertilizations, respectively. The second, "dynamic method", computed uptake as the product of the turnover coefficient (k_2) and mean mass of N in mature needles *plus* any fertilizer N increment in new needles. It has been noted for agricultural crops that static estimates of ^{15}N fertilizer uptake generally are lower than those computed by the difference method (Recous et al. 1988) and that was the case here as well. Fertilizer uptake by the static ^{15}N method here gave values 25 to 32% lower than those computed by the difference method. Melin and Nômmik (1988), reporting on results of ^{15}N experiments on Scots pine and Norway spruce, discuss this effect also but present no explicit comparative data. Jansson and Persson (1982) suggest a primary reason for the discord between difference and ^{15}N dilution estimates lies in the mineralization-immobilization turnover (MIT) of soil inorganic N. This phenomenon dilutes ^{15}N abundance in soil ammonium and thus the plant root system "sees" a lower abundance source. MIT essentially violates the assumption of instantaneous mixing required for the use of any dilution calculation. Since MIT can only reduce the ^{15}N abundance of the available N pool it follows that fertilizer N uptake affected by this phenomenon must be underestimated.

The second, or dynamic, estimate of uptake yielded higher values in both seasons of application (Table 5-5). These estimates rely on the time-integrated PDF of the soil ammonium pool itself and therefore are more comparable to the estimates of total uptake of 101 and 83 kg ha^{-1} in spring and fall, respectively. Both ^{15}N estimates deviate significantly from the total uptake but the direction of the deviation is seasonally-dependent. This reflects mainly the differential in turnover rates calculated for spring and fall (Table 5-3). These rates were responsive primarily to N arriving at needles from the roots. Nitrogen translocated to needles from more local sources (e.g. older foliage, twigs, branches) prior to the appearance of labelled N in xylem sap would not be taken into account. This is consistent with the concept of a mobile internal pool of N and explains also the fact that peak concentrations of spring-fertilized trees occurred prior to the peak in ^{15}N enrichment. Rate of uptake in fall-fertilized trees by the dynamic method gives the result more often obtained in tracer studies: fluxes as estimated from changes in standing stocks are underestimates because cycling is occurring through a pool whose size is regulated. In general the rates measured by this latter method lend credibility to the other uptake estimates presented because they were derived with much less dependence on the allometric regression equations. Fluxes were estimated only from the turnover coefficient and an estimate of the mean mass of foliage N. No differences were calculated on estimates generated by the regression equations.

Turnover

Fertilizer N was initially not uniformly distributed among foliar cohorts (Fig. 5-3). This effect has been noted previously for slash pine (Mead and Pritchett 1975), Douglas-fir (Heilman et al. 1982), Norway spruce and Scots pine (Nômmik 1966). Although PDF in current and one-year-old cohorts was significantly different on a statistical basis, the magnitude of the difference is surprisingly small considering that older tissues contained over 1% by mass N of natural abundance that would dilute incoming fertilizer N. If, for example, the internal source of N for new and one-year-old needles of spring-fertilized trees is assumed equal at a PDF of 0.17 (the maximum enrichment observed in any foliar tissue) it may be calculated that the N in the older tissue would have to have received a minimum of 0.56 times its mass in order to attain the PDF of 0.075 observed after 6 months (Fig. 5-3). This rate of turnover is almost four times the estimate in Table 5-3. The pattern of labelling cannot have been generated solely by a cascade system from older to current foliage because this arrangement produces initially higher enrichment in the first element of the system (Sheppard 1962). Nor can the results be explained by a single common source supplying needles of kinetically homogeneous N since this arrangement would create a much larger ^{15}N increment in current, versus one-year-old, foliage than was observed.

The distribution of label between age classes appears to require the existence of at least two kinetically-distinct pools of N in foliage and at least two sources of N for developing foliage. Such a system would allow rapid turnover of N in any foliage and provide to the newest foliage N of a different labelling intensity than that available to other cohorts. A biochemical basis for two kinetic fractions of foliar N can be found in the the types of compounds comprising the majority of cellular N. Broadly speaking N may be divided into that associated with metabolic processes, chiefly in enzymes involved in photosynthesis and intermediary energetic pathways; and macromolecules forming permanent structural elements such as cell walls. Two sources of N for new foliage are easily suggested by fundamental morphological considerations. First, N in developing shoots may be forwarded directly by the tissues to which it is attached - the twig and needles of the previous year's shoot. Second, N may arrive in the transpiration stream and ultimately derive from uptake or retranslocation from a more distal component. Although it is clear that multiple entry points exist for xylem N, from the standpoint of the foliage these are opaque. It is therefore justified to combine these sources for the purpose of investigating N dynamics in foliage.

A theoretical argument for the existence of a dynamic pool of N in conifers has been offered by Fagerström and Lohm (1977) and is consistent with the behaviour of foliar N in this work, provided that there exists a mechanism for regulating flow differentially to various sinks. Habib et al. (1988) proposed that N transfers within peach trees could be described by linking N demand to production of dry matter in different tissues that differ in their abilities to retain N. Whereas this explains the differential consumption of N by tissues of different growth rates it does not necessarily account for the flux of N through tissues that no longer possess the biological capacity to grow, viz. one-year-old foliage. Some accretion of N in one-year-old needles did occur but not enough to explain the turnover estimates, which were estimated under conservative assumptions at 30 to 54% annually.

An absolutely critical piece of evidence regarding the arrangement of internal N pools in Douglas-fir is the fact that in both seasons of application the maximum ^{15}N enrichment was found in the first cohort to develop fully *after* fertilization. This maximum enrichment occurred at the same time (late May 1983) for both treatment groups (Fig. 5-3). It is unequivocal that at least one source of N for this 1983 cohort had to be enriched at a minimum PDF of approximately 0.175. The most plausible candidate for such a pool would be the xylem sap itself but, if this were so, the 1982 cohort of spring-fertilized trees should be the most enriched. Therefore the primary source of N for new cohorts could not be the xylem sap that recently resided in roots. Further, the source could not be the total N in one-year-old needles because the ^{15}N enrichment never reaches the level of the 1983 tissue. The results can, however, be rationalized by postulating that the N that we observe in a needle is in fact composed of two kinetically-distinct pools that are lumped under the analytical procedure. The rapid turnover pool quickly becomes highly labelled as xylem sap from roots arrives, but the ^{15}N abundance of the total needle N remains modest due to the presence of a pool of immobile native N. Due to its proximity to developing buds, and connection to the vascular system, this high-turnover N pool becomes the probable source of N for new foliage. A new cohort becomes highly-labelled because *all* of its N, structural and dynamic, would be derived from high turnover pools. A conceptual model which accounts for all the above observations is presented in Figure 5-8. In the absence of detailed biochemical characterization of the forms of N involved, internal pools are designated merely as mobile or structural. "Other structural N" undoubtedly lumps some active pools such as fine roots but there was little in the patterns of tracer N of foliage to suggest major interchange with another distinct pool. This may indicate, as suggested by Nambiar (1987), that N immobilized by growth of fine roots is not retranslocatable.

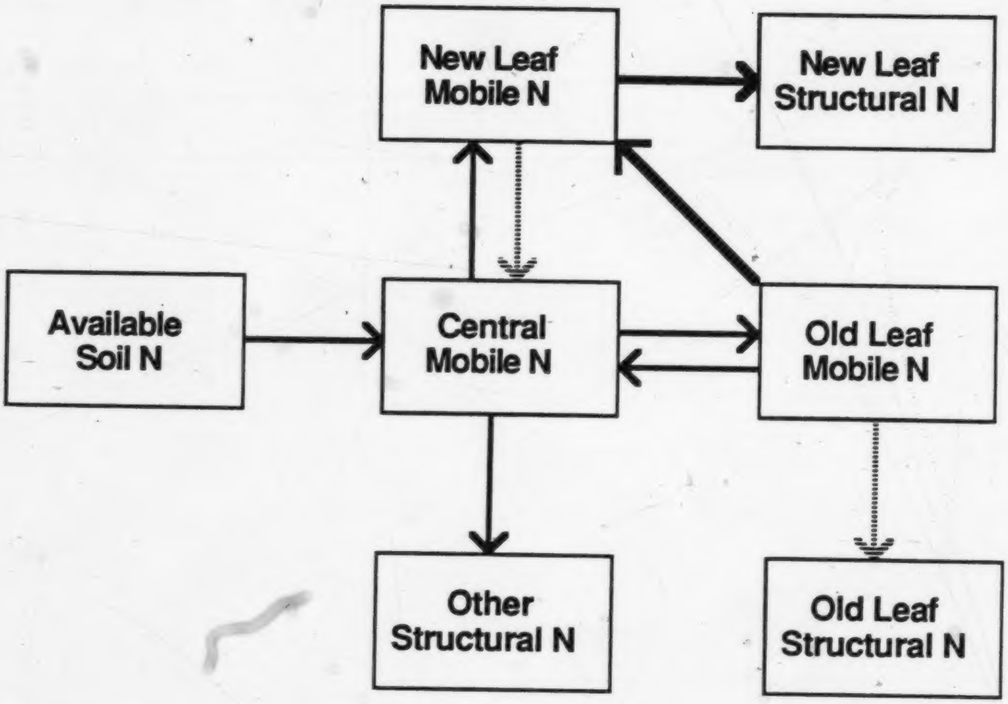

New Leaf Mobile N
New Leaf Structural N
Available Soil N
Central Mobile N
Old Leaf Mobile N
Other Structural N
Old Leaf Structural N

Figure 5-8. Conceptual model of N cycling within Douglas-fir during the first year after N fertilization. Dotted arrows indicate minor processes. Heavier arrows indicate strong directional flow occurring during the first few weeks after budbreak. Central Mobile Pool includes N in xylem sap. Retranslocation from New Leaf Mobile Pool to Central Mobile Pool is proposed to increase after the formation of a newer cohort.

The ^{15}N data suggest that N turning over through one-year-old foliage may be associated with a product designated for export to another plant component. Van den Driessche and Webber (1975), and Margolis and Waring (1986) studied changes in N fractions of Douglas-fir seedlings in response to N fertilization and both groups reported for needles a greater proportional increase in free amino acids than total N. Further, Margolis and Waring (1986) reported pools of amino acids fluctuated seasonally, with pronounced peaks occurring before budbreak and in late fall. These observations taken with the present data suggest that the high turnover of N in one-year-old needles reflects both their high photosynthetic rate (Brix 1983) and role in supply of amino acids for other regions of high demand such as fine roots and elongating shoots.

5.5 Conclusions

Fertilization of 38-year-old Douglas-fir with ^{15}N-enriched urea in spring and fall resulted in the appearance of ^{15}N in needles within 3 weeks irrespective of season of application. Estimates of rates based on turnover in one-year-old foliage indicated that uptake was approximately twice as fast for fall-fertilized, than for spring-fertilized trees. The majority of this uptake in fall fertilized trees had occurred by the next spring which, when considered alongside the pattern of fertilizer N availability, indicated that uptake had occurred throughout winter. It was estimated that after one year, approximately 15 and 21% of the applied N resided in foliage for spring and fall fertilizations, respectively. These recoveries were 25 and 32% lower than those estimated by mass balance of N in crowns. The discrepancy in estimates is most likely due to the complicating effect of mineralization-immobilization turnover in soil. Based on tracer dynamics in foliage total uptake after fall fertilization was approximately 130 kg N ha^{-1} in the first year. This estimate exceeded that calculated by mass balance by about 50 kg ha^{-1} and showed that N was turning over rapidly in needles. In contrast, the estimate of total uptake in the first year after spring fertilization was smaller than that computed by mass balance. This paradox could be resolved by invoking the existence of a mobile pool of N, temporally uncoupled from root xylem sap, but proximal to emerging shoots and capable of donating strongly to the growing meristem. The pool is proposed to be comprised of metabolically active N, likely N-rich amino acids, in older foliage and twigs. The proposed arrangement is consistent with data from fall fertilization where, unlike the spring-fertilized case, maximum concentrations and ^{15}N abundance occurred synchronously.

We predicted that cooler temperatures and greater soil moisture in fall would increase the ability of conifer roots and associated mycorrhizae to compete with soil heterotrophs for uptake of ammoniacal N, and therefore result in a higher fertilizer efficiency for fall-applied versus spring-applied urea. The results obtained are in agreement with this prediction. Fertilizer N availability appears to be regulated in this system primarily by the mineralization-immobilization dynamics of the soil microbiota. Any temporal variation in the inherent capability of the Douglas-fir root system for absorption of mineral N appeared to be of secondary importance in determining uptake rates.

Estimates of turnover in the second year after fertilization and beyond suggest that internal cycling was increased. This supports the contention of Nambiar and Fife (1987) that retranslocation in conifers is properly viewed from the standpoint of the N demands of active tissues, which increase in mass as N availability is raised.

5.6 References

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6. DISTRIBUTION AND TRANSFORMATIONS OF N AFTER SPRING AND FALL APPLICATION OF AMMONIUM NITRATE AND ^{15}N UREA TO A DOUGLAS-FIR ECOSYSTEM.

6.1 Introduction

Fertilization of coniferous forests with nitrogen is a common silvicultural practice in Scandinavia and has been carried out with some success in the U.S. Southeast and Pacific Northwest. In British Columbia and the U.S. Pacific Northwest the species most often treated is Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Regionally, Douglas-fir responds positively to N fertilization (Gessel 1984) but forest managers are often deterred by the poor predictablility of growth response (Ballard 1984).

Stand and site factors contribute to response variation (Edmonds and Hsiang 1987) but treatment variables are important also. Two treatment variables which can easily be adjusted are timing and chemical source of N. Ammonium nitrate and urea are the fertilizers normally considered practical and cost effective whereas spring and fall represent viable options for timing of application.

Ammonium nitrate has become the dominant fertilizer material in Scandinavian forestry (Malm and Möller 1975) and has generally compared favourably to urea in North American trials (Dangerfield and Brix 1981, Harrington and Miller 1979) but its lower N analysis compared to urea translates into greater cost in application. On the other hand, potential problems exist with the chemical reactivity of urea when applied to forest soils that can lead to volatile loss (Overrein 1968) and high rates of immobilization (Salonius and Mahendrappa 1979). This latter point is particularly germane for it is not known to what extent immobilized urea-N is made available through re-mineralization.

Nitrogen-15 tracer studies have been conducted in the laboratory to shed light on the short term fate of urea added to forest soils. It was reported that at moderate rates of addition microbial respiration and mineralization of native N increased while urea-N was immobilized. At higher rates of addition (200 to 400 kg N ha^{-1}) immobilization dominated and was partially abiotic (Foster et al. 1985). The long term fate of immobilized N was not described in this work.

Timing of N fertilizer applications brings into play climatic and soil conditions as well as phenology. From a standpoint of urea fertilization of Douglas-fir, fall appears more suitable because lower temperatures and greater soil moisture should reduce volatile loss (Watkins et al. 1972) and possibly limit chemical side-reactions (Foster et al. 1985). On the other hand, maximum root activity is expected in spring and this should correlate to maximum uptake potential for trees. Ammonium nitrate, because of the leachability of the nitrate ion, is generally thought to be better suited to application in spring.

The present research was undertaken to examine the availability of AN and urea in both spring and fall applications. Urea was enriched in the stable isotope ^{15}N which permitted a quantification of the fate of urea N and estimation of some cycling rates. Previous ^{15}N field studies in forest soils have focussed on the fate of added N (Mead and Pritchett 1975, Heilman et al. 1982). Our objective was to use ^{15}N to permit a kinetic description of N cycling after fertilization. We hypothesized that immobilized ^{15}N would not be kinetically homogeneous.

6.2 Materials and Methods

Experimental Design

The study site and experimental design are described in Chapter 2.

Sampling

At intervals shown in Table 6-1 soils were sampled to a depth of 30 cm using an impact corer (Jurgensen et al. 1972) of 57 mm inner diameter, at nine grid locations established by orthogonal trisection of each plot. Samples were composited within plot by horizon (forest floor) or by 10 cm depth increment (mineral soil). If a coarse fragment of sufficient size to stop the sampler was contacted on the first coring attempt at a given node, a second core would be taken within 20 cm laterally. If a second attempt failed to yield an entire core the missing depths would be recorded and sampling would resume at the next node. All forest floor and 0-10 cm composites consisted of the full complement of 9 cores but at 10-20 and 20-30 cm depths one or two cores per plot often were missing. Samples were also taken from the 30-40 cm depth with a bucket auger but these occasionally were contaminated with needle litter which had fallen in from the edges of the hole made by the impact corer. These samples were judged too unreliable for general use in ^{15}N analyses and are referred to only when needed to clarify mass balance issues.

Forest floor samples were air-dried and ground to pass a 2 mm sieve in a Wiley mill. Mineral soils were air-dried and passed through a 2 mm sieve prior to analysis.

Periodic measurements of carbon dioxide evolution from the soil surface were made by the soda-lime method (Edwards 1982). Four randomly-located subplots were established within each of the control and urea-fertilized plots and two alternate, closed respirometers were positioned in each. Each respirometer consisted of an inverted PVC cube (13.6 cm sides) with a missing side oriented downwards that had been cut into the forest floor using a sharp knife. The side facing upward had a circular hole cut in it large enough to accomodate a No. 13 rubber stopper. Five g of dried, preweighed soda lime was placed in a 7 cm diameter glass Petri dish, located within the respirometer, the rubber stopper firmly secured and allowed to collect CO_2 for a period of 48 hr. At the end of this time the soda lime was returned to the laboratory, dried and weighed. Subsequent measurements would make use of the alternate respirometer, which had been left open and allowed to receive precipitation, and exchange heat and gases with the atmosphere. The CO_2 absorbed by soda lime was computed from the gain in mass after making the adjustment for water suggested by Howard (1966).

Table 6-1. Timetable for soil sampling.

	Time after Application (Weeks)		Fertilizer Treatment				
Date	Spring-applied	Fall-applied	Control	Spring Urea	Spring AN	Fall Urea	Fall AN
June 11/82	3	-	*	*	-	-	-
July 9/82	7	-	*	*	-	-	-
Dec 13-16/82	29	3	*	*	*	*	-
Feb 24/83	40	13	*	*	-	*	-
June 8-10/83	54	28	*	*	*	*	*
Sept 2/83	-	40	*	-	-	*	-
Nov 18/83	-	51	*	-	-	*	*
May 24/84	105	-	*	*	*	-	-
Nov 8/84	-	102	*	-	-	*	*

Laboratory Analysis

Total carbon was determined on mineral soils by oxidation at 1300°C in an O_2 stream followed by infra-red CO_2 detection (LECO Carbon Determinator CR12, Model 780-000). Mineral nitrogen in soil samples was extracted with 2M KCl (Keeney and Nelson 1982) using a 5:1 or 10:1 solution to soil ratio for mineral soils and forest floors respectively. Ammonium and nitrate in extracts from unlabelled soils was measured using standard AutoAnalyzer II methods (Technicon Ltd 1977a and b). Ammonium and nitrate in KCl extracts of soils enriched in ^{15}N were determined by steam distillation into 2% boric acid followed by titration with 0.01 or 0.05M H_2SO_4 (Keeney and Nelson 1982). The soil residue from extraction was washed with 0.01M KCl, dried, milled to pass a 0.25 mm mesh sieve, and analyzed for total Kjeldahl N (Bremner and Mulvaney 1982), again determining N by steam distillation.

Titrated distillates were acidified with H_2SO_4 and dried at 55 °C in preparation for mass spectrometry. Ammonium sulfate salts were oxidized with LiOBr (Porter and O'Deen 1977) and the 29/28 ratios of the resultant dinitrogen determined in a Micromass 602C dual inlet stable isotope ratio mass spectrometer.

Data Analysis

For mineral soil, mass per unit area was calculated in the normal way using plot-specific bulk densities that had been adjusted for the coarse fragment content. This procedure considered the fine earth fraction as expanded to include space occupied by coarse fragments and resulted in conspicuously low bulk densites (Chapter 2). Mass of N and ^{15}N in the forest floor was calculated as the product of the concentration and mass of sample divided by the sampling area. The proportion of N due to fertilizer was calculated as the quotient of the ^{15}N excess in the fraction of interest and the ^{15}N excess of the fertilizer source.

Recovery of fertilizer N was calculated by difference and ^{15}N dilution methods. The difference method calculated recovery as the difference in mass of the N fraction of interest in fertilized and control plots divided by the fertilizer N dosage. Recovery by ^{15}N dilution was the product of the proportion due to fertilizer and mass of N in the fraction of interest divided by the fertilizer N dosage. "Primed" NH_4^+-N (kg ha^{-1}) was computed by taking the difference between recovery estimates by the difference and ^{15}N dilution methods and multiplying the result by the fertilizer N dosage.

Comparisons among controls and fertilized plots were performed, where appropriate, by multivariate ANOVA in the MGLH module of SYSTAT (Systat Inc. 1986). Nonlinear least squares fitting was performed both in the NONLIN module of SYSTAT and PCNONLIN (Statistical Consultants Ltd 1985). Both programs used a modified Gauss-Newton algorithm for minimization of squared residuals. Simulations were performed in STELLA (High Performance Systems Ltd 1985), a graphically-oriented software package for the Apple Macintosh computer. A second-order Runge-Kutta numerical integration scheme was employed.

6.3 Results and Discussion

Recovery of Fertilizer N

Analysis of variance (ANOVA) on total recovery estimates (summed over all depths), performed by dropping observations at 7 and 13 weeks that were thought to be separated by too great a difference in time of sampling between seasons of application, showed time to be highly significant ($P<0.0001$) but the season by time interaction had a probability of only 0.16. Thus, an important decline in recovery occurred under both seasons of application (Table 6-2) but evidence for a difference in gross retention of ^{15}N was weak. Soil recovery of fertilizer N in all forms was maximal 3 weeks after application and declined over the following two years to approximately 50 and 57% for spring and fall applications, respectively (Table 6-2). Recovery at 3 weeks under fall application exceeded

Table 6-2. Recovery of fertilizer N in soil after application of N as ^{15}N-urea at a dosage of 200 kg ha^{-1} in spring and fall.

Treatment	Weeks after Application	^{15}N in stratum as % of applied				
		LFH*	0-10 cm	10-20 cm	20-30 cm	Total (SE)
Spring	3	50.1	25.8	13.5	2.5	91.9 (10.9)
	7	36.6	19.6	5.0	3.8	64.8 (7.1)
	29	32.7	22.2	5.3	2.3	62.5 (5.6)
	40	29.2	19.8	4.5	2.1	55.6 (2.6)
	54	23.4	18.2	4.9	2.9	49.4 (6.1)
	105	30.0	14.4	4.0	2.1	50.4 (2.4)
Fall	3	36.9	57.9	18.5	6.9	120.2 (11.5)
	13	24.6	34.1	14.2	6.0	78.8 (3.8)
	28	24.2	26.4	9.4	6.3	66.3 (11.4)
	40	20.6	17.4	7.6	5.5	51.2 (8.7)
	51	22.5	27.7	7.2	6.0	63.4 (14.3)
	102	20.7	22.3	8.4	5.5	56.9 (14.1)

*sum of recoveries in L, F and H horizons of forest floor the amount applied by 20%, which suggested a heterogeneous distribution of ^{15}N. Throughout the experiment over 80% of fertilizer N in soil was retained in the combination of the forest floor and 0-10 cm layer, and only small amounts of ^{15}N were found below 20 cm at any time. This suggested that ^{15}N was not subject to extensive leaching and reductions in total recovery reflected primarily plant uptake and gaseous losses. Volatile loss of N as NH_3 after spring fertilization (Chapter 3) was estimated at 28 kg ha^{-1} of which about 60% was from fertilizer sources. If the 17 kg of fertilizer N from this process is added to the inventory at 2 years after fertilization the estimates of fertilizer recovery in the two seasons of application are identical.

Coarse fragments were a persistent problem in estimation of the ^{15}N mass balance. The high proportion of cobble in some plots tended to skew sampling frequency to microsites where fewer cobbles were present. Water flow alterations caused by large coarse fragments have been reported (Childs and Flint 1988) and may have been a factor here. Water flow during heavy precipitation may be channeled to regions of the soil where coarse fragments are fewer and thereby enrich such areas in fertilizer N for a period. It was noted above that soils in cobble-dense plots had high concentrations of organic matter in the fine earth fraction. This would tend to preserve heterogeneity which developed initially from oriented water flow.

Differences existed between seasons of application when fertilizer recovery was examined by depth (Table 6-2). When data were subjected to ANOVA with both depth and time as split-plot factors, significant interactions ($P<0.001$) were found for the three-way and all two-way interactions. This was taken as conclusory evidence that the distributional behaviour of fertilizer N did differ between seasons of application. More fertilizer N was retained in the forest floor on both an absolute and relative (within profile) basis after spring fertilization. For the fall-fertilized plots the greatest proportion of applied N was found in the 0-10 cm layer in every case except September 1983 (week 40) when the amount in the forest floor was about equal. The greater penetration of fertilizer N in fall appeared to be caused by the much greater rainfall; which, in the first week after fertilization, was about 40 times that occurring in the corresponding period after spring fertilization (Table 6-3). In the first month after fall fertilization approximately 29 cm of water was available for leaching of fertilizer N. Temperatures were lower also (Table 6-3) and this likely contributed to lower rates of ureolysis, which would enhance the mobility of urea. Despite these considerations, complete recovery was obtained for fall-applied urea at 3 weeks (Table 6-2). It was concluded that leaching of urea-N was not a significant process in this system.

Variability in recovery estimates described above, although considerable, is in-line with reports from other forest soils (Mead and Pritchett 1975, Heilman et al. 1982, Nambiar and Bowen 1986, Melin and Nômmik 1988) and even agricultural systems (Harmsen and Moraghan 1988, Recous et al. 1988). Percentages of applied urea-N recovered in soil after two years (Table 6-3) were

Table 6-3. Throughfall and soil temperature at 0 cm depth during the first month after spring and fall fertilizations.

	Season of Application			
	Spring		Fall	
Weeks After Application	Cumulative Throughfall, mm	Mean Soil Temperature, °C	Cumulative Throughfall, mm	Mean Soil Temperature, °C
1	2.4	7.8	93.4	3.5
2	5.8	9.5	94.3	2.5
3	6.4	9.7	195.3	2.1
4	6.4	14.0	286.3	1.8

higher than recoveries reported by Heilman et al. (1982) and Pang (1985) for field and potted soils, respectively, supporting the growth of young Douglas-fir; but slightly lower than the 62% reported by Melin and Nômmik (1988) for a 50-year-old mixed Scots pine/Norway spruce stand.

The strong retention of urea-N in this system was a function of the organic soil components and root systems. The solubility of urea in water is such that all applied urea could potentially dissolve in the soil water stored in the forest floor and surface mineral soil (Chapter 3) and urea, being uncharged, is highly mobile in soil (Rachhpal-Singh and Nye 1984). Without ureolysis, urea could pass through the system. Evidently, very high ureolytic capacity existed in the forest floor and surface mineral soil. The importance of the forest floor as a sink for fertilizer N has been emphasized for boreal systems (Overrein 1967, Foster et al. 1985). The forest floor was important here also but was capable of retaining, at most, 50% of the applied urea-N (Table 6-3). The Ahe horizon had over 10% organic matter on this site and, after fall fertilization, was an equally important sink for urea-N.

Transformation and Transport of Fertilizer N

Spring Patterns

Nitrate

Nitrate concentrations were low in all soils throughout the period of observation. Nitrate-N was added at 100 kg ha^{-1} in the AN treatment and there must have been a period of high nitrate concentrations in these plots. However, mineral N concentrations were examined on only three occasions in the AN treatment; the first sampling occurring 6 months after fertilization. By this time nitrate concentrations had declined to control levels in all samples save the forest floor in one replicate, which averaged 10 mg kg^{-1} nitrate-N (data not shown).

Nitrate-N in KCl extracts of urea-fertilized soils in this study was often near the limit of detection for the distillation method used. The ^{15}N abundance was measured on any occasion where at least 50 µg of putative nitrate-N was distilled from the sample extract. Several lines of evidence indicated that the analyte concentrations were a consequence of a real soil nitrate pool and not analytical noise. First, the concentrations were greater than those in control plots which, by the continuous flow procedure used (Technicon Ltd 1977b), were below detection and could not have exceeded 0.5 mg kg^{-1}. Second, significant differences existed between sampling times when data were analyzed by one-way ANOVA. Third, the proportion due to fertilizer in this fraction declined with time (Fig. 6-1), as expected had the analyte been derived from nitrification of soil ammonium. Finally, the titration values obtained after treatment with Devarda's alloy could not be explained by carryover of residual ammonium because the distilled N was not equal in ^{15}N abundance to the ammonium, nor did the ^{15}N abundance form a constant ratio to that of ammonium. Nitrate contamination of glassware was not a problem because titers of blanks were always negligible. It thus appears that urea fertilization resulted in some stimulation of nitrification although no appreciable *accretion* of nitrate ever occurred. The potential significance of this phenomenon is further discussed later in this chapter, after consideration of patterns in mineralization and immobilization.

Mineralization-Immobilization

Control ammonium concentrations fluctuated significantly over time only in the forest floor, which generally was approximately five times that found in the mineral soil (Fig. 6-2). In the LF horizons a peak was seen in mid-winter (40 weeks) that may have been related to decomposition of litter from the previous fall. A peak in the H horizon that occurred in spring may have been related to displacement of ammonium from the LF complex. In control mineral soil, highest concentrations of ammonium were recorded at the 0-10 cm depth as expected.

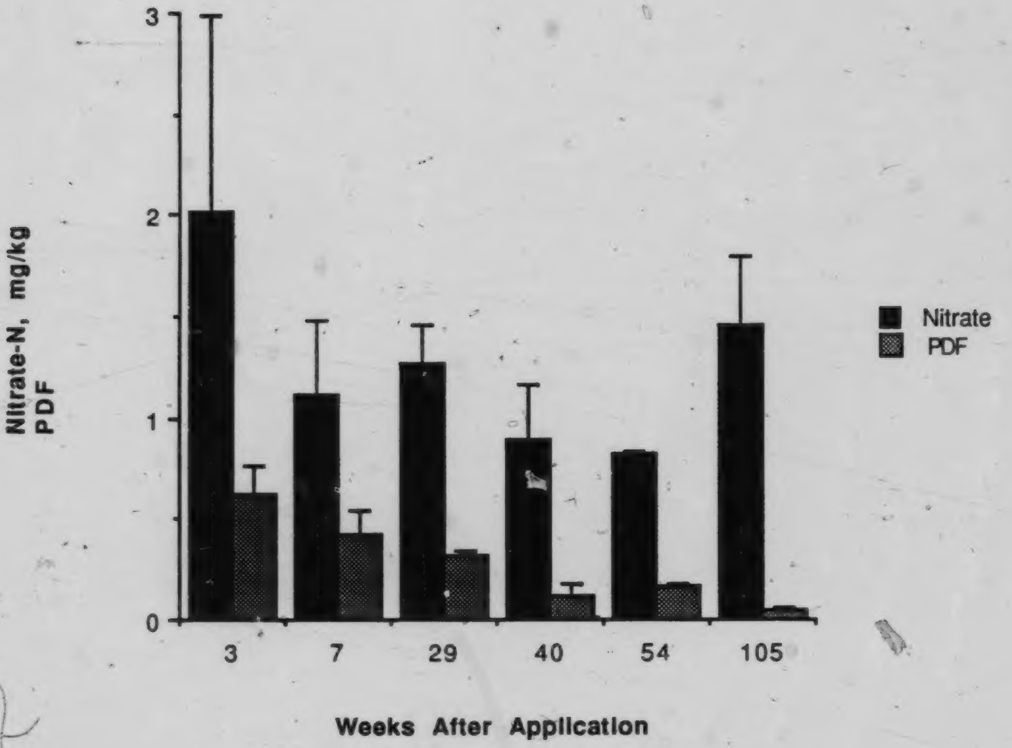

Figure 6-1. Concentration and proportion due to fertilizer (PDF) of nitrate-N at 0-10 cm depth after spring application of urea. Error bars indicate 1 standard error.

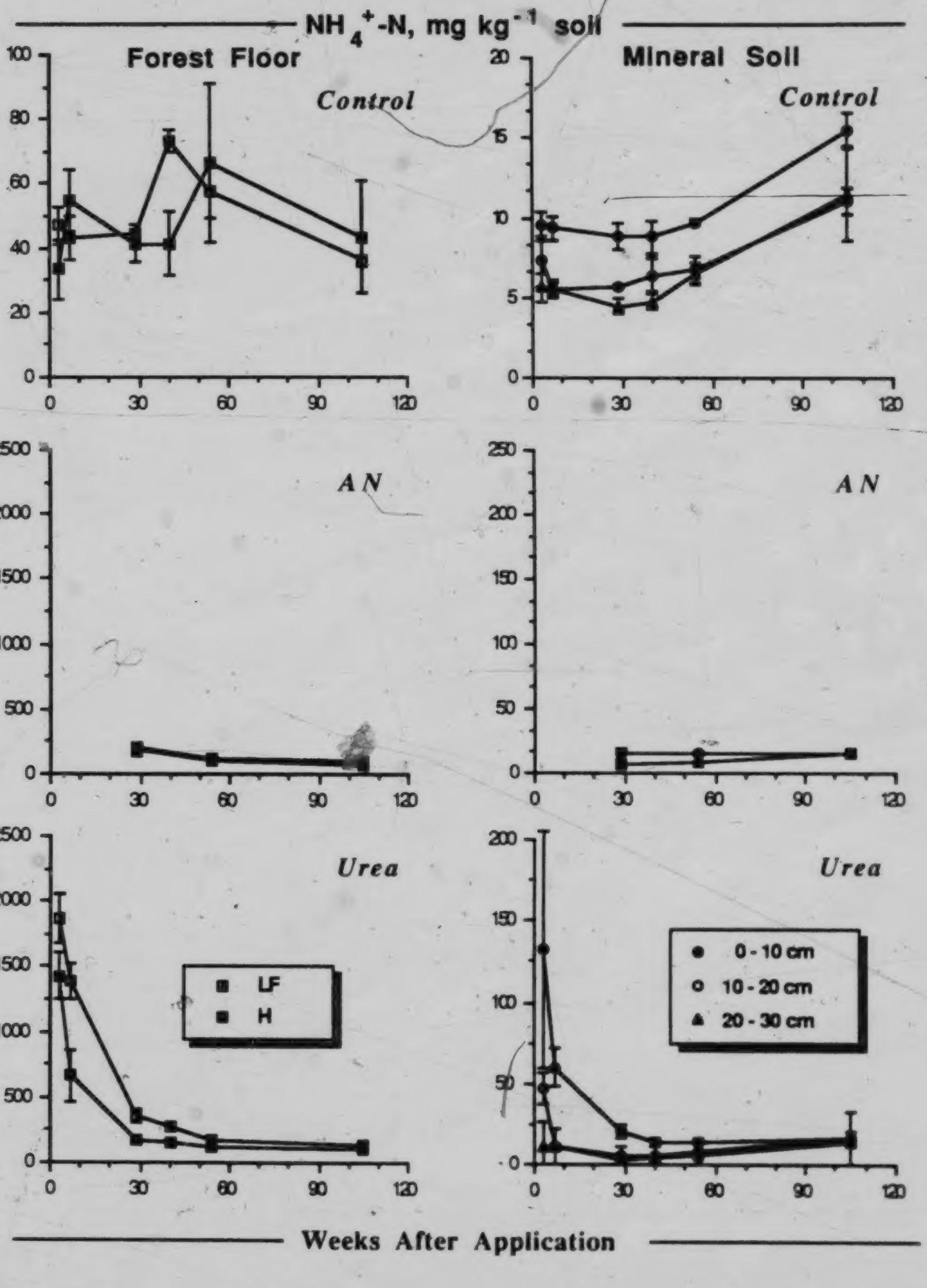

Figure 6-2. Concentration of ammonium-N in forest floor and mineral soil of controls and soils fertilized in spring. One arm of an error bar equals 1 SE.

Concentrations varied in parallel at all depths examined and rose towards the end of the study period.

Ammonium nitrate fertilization had raised ammonium concentrations approximately four-fold 6 months after fertilization (Fig. 6-2, Table 6-4) but there remained a significant ($P<0.001$) increase over control in only the L and F horizons at the end of two years. Undoubtedly, mineral N concentrations were elevated a great deal more throughout the first 6 months but observations were not made in this period. On the other hand, fertilization with urea in spring resulted in extremely large increases in ammonium concentrations to a depth of 20 cm (Fig. 6-2). Of the mineral N remaining after 6 months, more was in the forest floor of urea treatments. Concentrations in the forest floor at 3 weeks after fertilization approached 2000 mg kg^{-1}, which were about 40 times those in controls. Concentrations declined exponentially in the forest floor such that, at 6 months after fertilization, only about 16% of the amount of ammonium recorded at 3 weeks remained. This N was not generally accounted for by leaching to the mineral soil because concentrations there followed a similar pattern of decline (Fig 6-2). Rather, the majority of inorganic N in mineral soil was present already at 3 weeks after fertilization. Precipitation was not available to leach fertilizer N to mineral soil during the first 3 weeks, so the accumulations of mineral N seen must have occurred as a result of diffusion alone. The low mobility of the ammonium ion and the general lack of nitrate suggested that N penetrated the forest floor in organic forms, probably largely as urea.

The recovery of applied N in inorganic form was similar for urea and AN (Table 6-5) but was low from 6 months after fertilization onward, averaging only 5%. Ephemeral elevations in the mass of available N after fertilization of forest soils has been reported for a diversity of forest soils (Johnson et al. 1980, Otchere-Boateng 1981, Nambiar and Bowen 1986, Melin and Nômmik 1988) and has been interpreted as due to rapid immobilization. This explanation is consistent with the pattern of availability reported here. An equivalent of only 14% of applied N was volatilized from urea whereas this

Table 6-4. Concentration (SE) of ammonium-N in forest floor and mineral soil after fertilization with urea and ammonium nitrate in spring.

Treatment	Weeks after Fertilization	LF	H	0-10 cm	10-20 cm	20-30 cm
		mg kg^{-1}				
Control	3	47.0 (4.9)	33.3 (9.1)	9.5 (0.9)	7.2 (1.6)	5.6 (0.9)
	7	43.3 (6.9)	54.7 (9.7)	9.3 (0.8)	5.5 (0.4)	5.5 (0.5)
	29	44.7 (2.8)	41.3 (5.8)	8.8 (0.8)	5.7 (0.1)	4.5 (0.5)
	40	73.3 (3.7)	41.3 (9.9)	8.8 (1.0)	6.4 (1.1)	4.7 (0.5)
	54	57.3 (8.2)	66.7 (24.7)	9.7 (0.2)	6.8 (0.8)	6.5 (0.7)
	105	36.0 (1.6)	43.3 (17.3)	15.4 (1.1)	11.0 (0.8)	11.5 (2.9)
AN	3	-	-	-	-	-
	7	-	-	-	-	-
	29	200 (25)	184 (40)	14.8 (4.5)	7.7 (0.8)	6.6 (0.3)
	40	-	-	-	-	-
	54	127 (21)	103 (43)	15.7 (2.2)	8.4 (0.8)	8.4 (0.9)
	105	109 (11)	64.3 (5.7)	16.0 (2.2)	16.0 (0.7)	15.1 (2.9)
Urea	3	1870 (186)	1430 (180)	132 (73)	46.2 (14.8)	9.9 (2.1)
	7	1380 (136)	660 (201.0)	59.8 (12.0)	11.2 (2.3)	10.5 (1.8)
	29	359 (49)	177 (12)	20.7 (3.6)	5.8 (0.7)	3.1 (0.9)
	40	276 (28)	162 (4.6)	13.8 (3.1)	5.6 (0.6)	4.7 (0.3)
	54	171 (7.7)	121 (6.1)	13.2 (1.0)	8.1 (0.6)	5.0 (0.1)
	105	131 (17)	103 (10)	16.3 (4.0)	16.6 (5.2)	13.7 (1.5)

Table 6-5. Recovery of N in soil inorganic forms (SE) after spring fertilization of Douglas-fir with urea and AN @ 200 kg N ha^{-1}.

	Fertilizer Source			
	AN	Urea		
	Recovery, % of applied			
Weeks after Application	Difference Method		^{15}N Method	"Primed" NH_4^+-N, kg ha^{-1}
3	-	62.0 (14.9)	49.9 (9.5)	24.2
7	-	34.7 (4.8)	23.5 (2.7)	22.4
28	4.9 (3.8)	5.9 (2.7)	4.6 (0.6)	2.6
40	-	3.3 (3.1)	3.0 (0.2)	0.6
54	2.3 (0.3)	1.4 (2.5)	2.1 (0.1)	-1.4
105	1.8 (3.4)	1.6 (4.9)	1.1 (0.1)	1.0

process was presumed negligible in AN-treated plots. Plant uptake (Chapters 3 and 4) could not account for more than 25% of applied N and there was no evidence for substantial leaching. Total recovery of soil tracer N though, was relatively high (Table 6-2).

It is important to note that, during the first 6 months, recovery estimates from difference calculations were consistently higher than those from ^{15}N dilution. The additional native NH_4^+-N present in urea-treated-plots, "primed" N, is presented in Table 6-5. For the first 2 months after urea fertilization the mass of native ammonium was approximately trebled. Most of this increase occurred in the forest floor (Fig. 6-3a).

Immobilization of urea-N was extremely rapid (Fig. 6-4) and accounted for approximately half the applied N. Because between plot variability was high, differences apparent in the graph were not significant on a statistical basis and net transfer of ^{15}N to organic N fractions was already complete at 3 weeks. An estimate of the immobilization rate was obtained by assuming that the size of the organic N pool did not change over 3 weeks, and that the ammonium immobilized had a ^{15}N abundance equal to the mean of the value at 3 weeks and the initial abundance calculated from fitting the ^{15}N abundance to a first-order decay function. This procedure showed that the immobilization had totalled 130 kg N ha^{-1} over the 3 week period (Table 6-6). The gross mineralization rate could then be calculated as 86 kg N ha^{-1} by assuming all mineral N that wasn't immobilized to have either volatilized or entered plant tissues. The latter rates had been estimated previously (Chapter 3, Chapter 5) at 28 and 6 kg ha^{-1} for the 3 week period.

Rapid immobilization after urea fertilization has been noted previously (Salonius and Mahendrappa 1979, Foster et al. 1985) and probably involves stimulation of the microbial community as a result of the solubilization of organic matter accompanying ureolysis (Foster et al. 1985). Respiration measurements, initiated 4 months after fertilization, showed no significant differences among treatments at that time (data not shown).

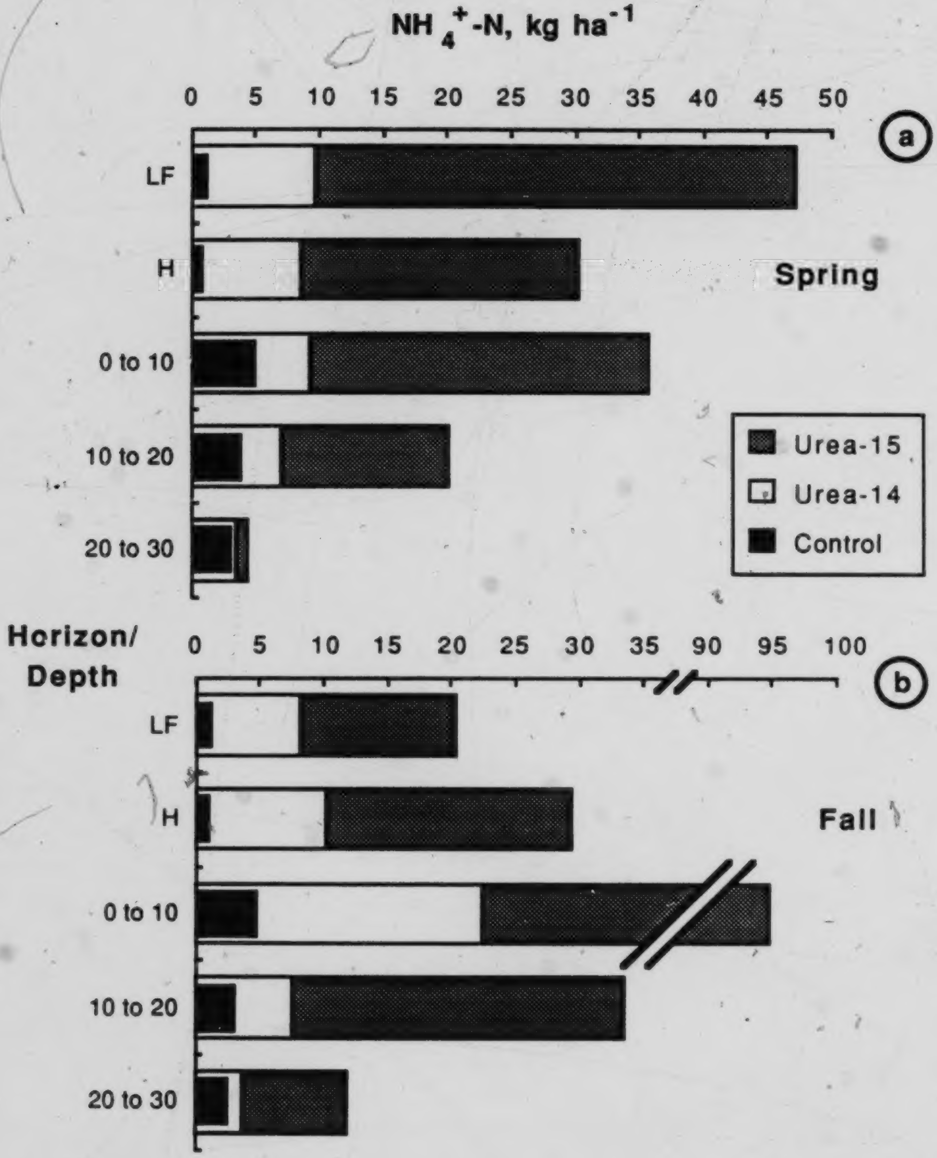

Figure 6-3. Mass of fertilizer and native N by depth 3 weeks after spring- and fall-application of ^{15}N urea@ 200 kg N ha^{-1}. "Primed" N indicated by difference between controls and "urea-14".

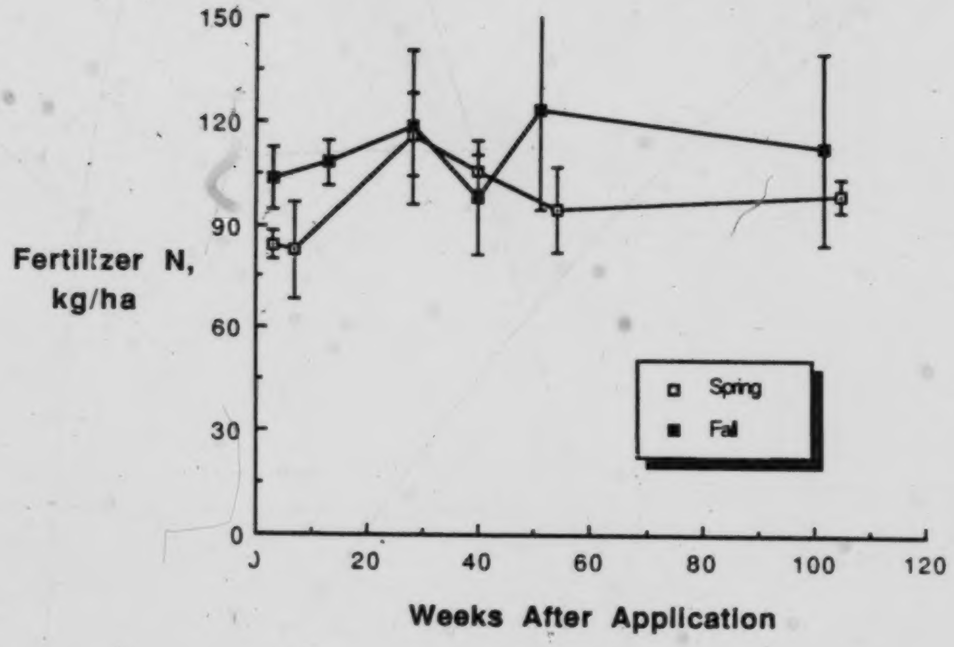

Figure 6-4. Immobilization of N applied as urea @ 200 kg N ha^{-1} to a forest soil supporting 38-year-old Douglas-fir. One arm on any error bar indicates SE for 3 plots.

Table 6-6. Estimates of gross N transfers (SE) in the first 3 weeks following spring and fall fertilization of 38-year-old Douglas-fir with urea-N @ 200 kg ha^{-1}.

	N Flux, kg ha^{-1}			
Season of Application	Immobilization	Mineralization	Volatilization	Plant Uptake
Spring	130 (21)	86 (14)	28 (3)	6 (2.7)
Fall	143 (10)	128 (13)	14 (0.2)	7.5 (1.5)

Forest floor pH did rise significantly in urea-treated plots (Fig. 6-5).

Fall Patterns

Nitrate

As was the case after spring fertilization, no significant accretion of nitrate occurred in any treatment. Highest concentrations were recorded in the 0-10 cm layer of the urea treatment (data not shown). The general pattern was the same as seen for spring fertilized-plots: maximum concentrations appeared in the first sampling after treatment and declined throughout the next year (Fig. 6-6). The labelling was again consistent with an ammonium source - ^{15}N enrichment paralleled that of the ammonium fraction. Nitrate formed in these systems must have a very short half-life. Despite the addition of 100 kg ha^{-1} nitrate-N in the AN treatments essentially none remained after 6 months. Plant uptake was the probable major fate for this N based on foliar N concentrations (Chapter 4). Nitrate from nitrification likely is fated for plant uptake also but little nitrification could be occurring given the immobilization potential of the system and the slow growth of nitrifying organisms (Schmidt 1982).

Mineralization-Immobilization

Concentrations of ammonium in the forest floor of control plots fluctuated about a mean of about 50 mg kg^{-1} (Fig 6-7). Peaks occurring in late fall probably corresponded to release from aboveground litter decomposition. In mineral soils of control plots concentrations showed no clear seasonal pattern and varied only between 5 and 10 mg kg^{-1} throughout the 2 year study period. A peak in control concentrations in May 1984 (Fig. 6-2) recorded for spring treatments escaped detection altogether under the sampling scheme for fall treatments.

Ammonium concentrations in AN-treated plots followed a pattern similar to that seen after spring fertilization (Figs. 6-2 and 6-7). Concentrations in surface horizons were about triple those of control at 6 months after fertilization but this increase was not

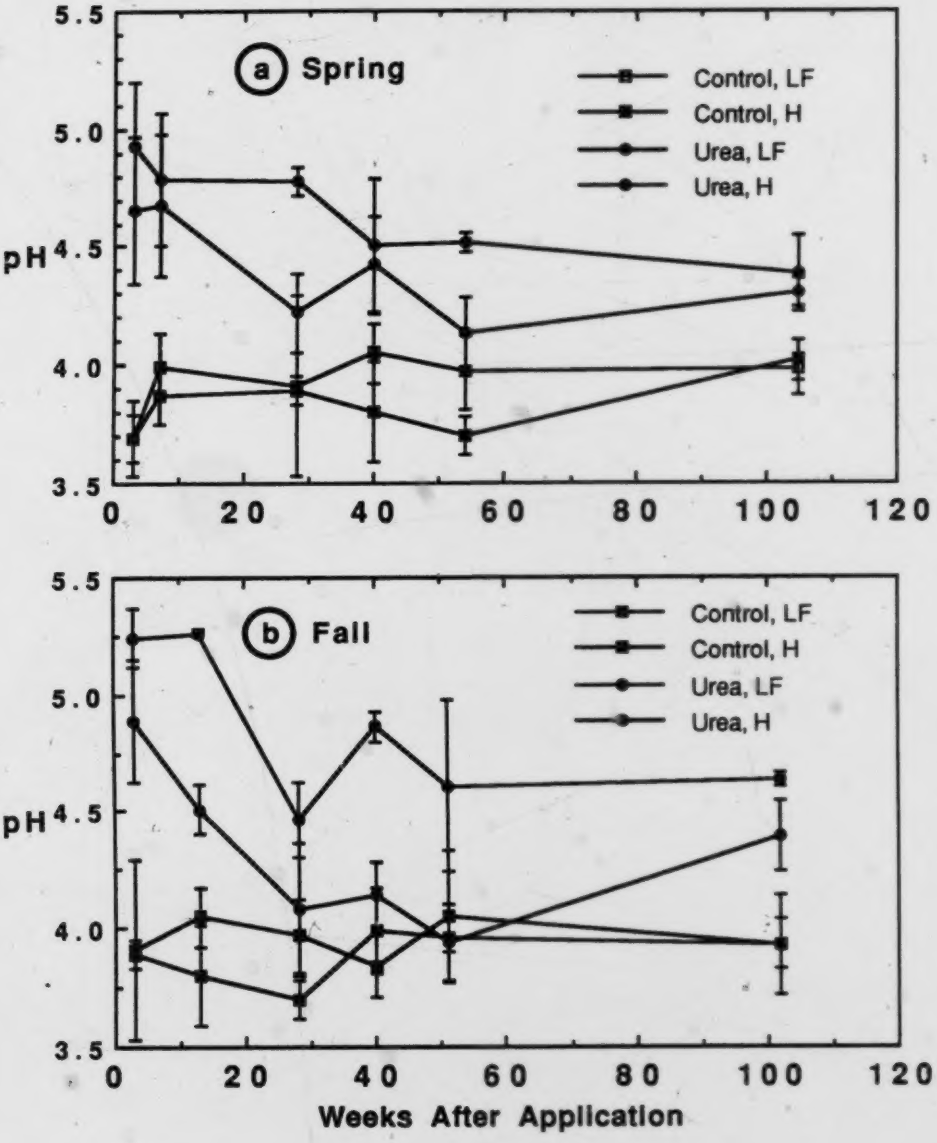

Figure 6-5. pH of forest floor after spring and fall application of urea-N@200 kg ha^{-1}. One arm on error bars indicates standard error of mean for 3 plots.

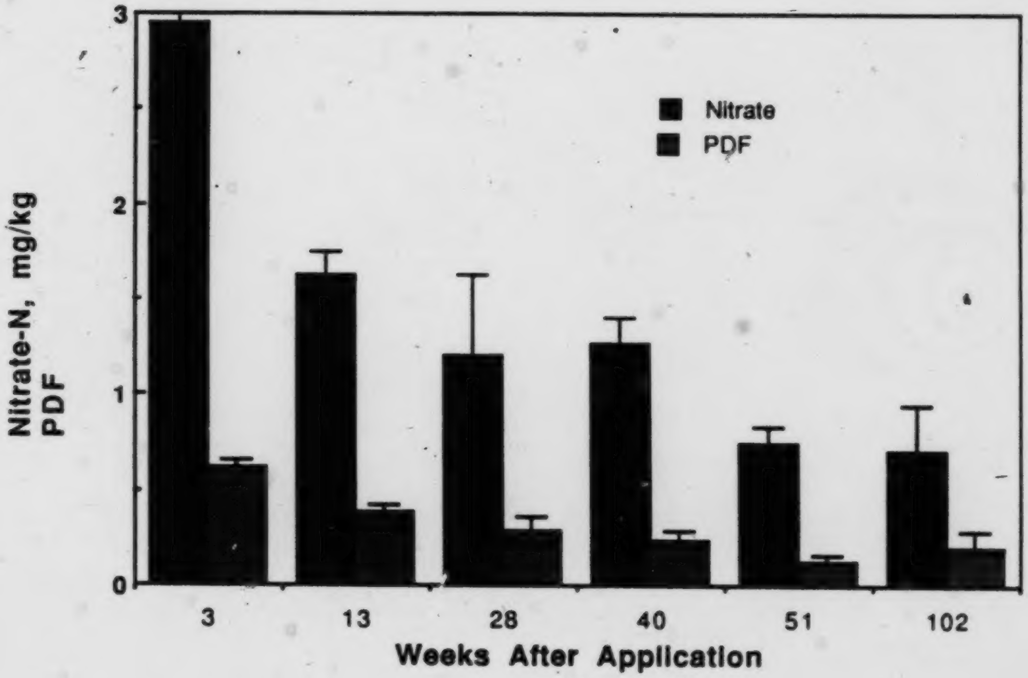

Figure 6-6. Concentration and proportion due to fertilizer (PDF) of nitrate-N in the 0-10 cm depth of soil fertilized in fall with urea-N @200 kg ha^{-1}.

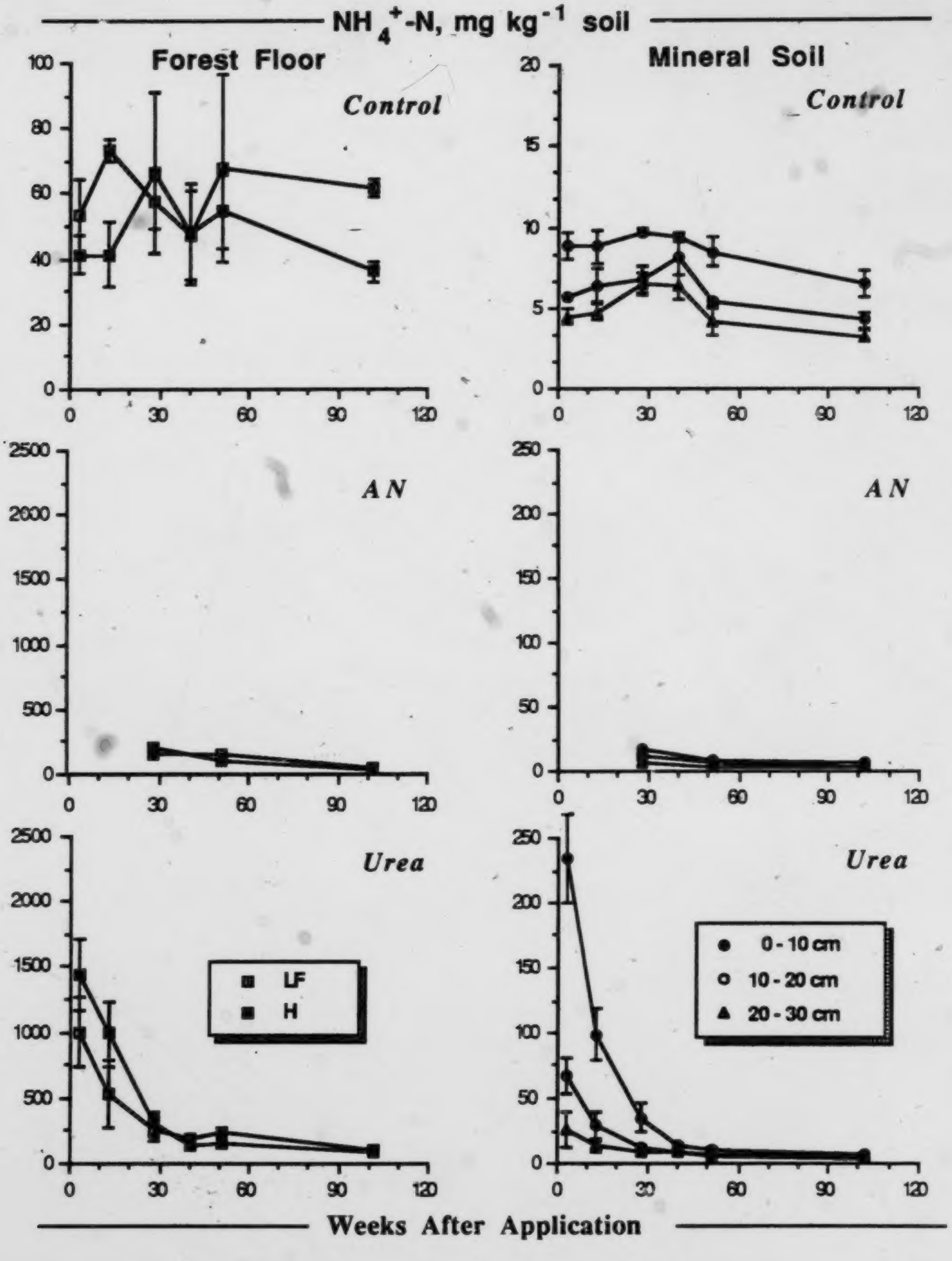

Figure 6-7. Concentration of ammonium-N in forest floor and mineral soil of controls and soil fertilized in fall. One arm of an error bar equals 1 SE.

maintained (Table 6-7). Urea fertilization resulted in higher elevations over control than did AN (Table 6-7) and, a significant effect remained in the forest floor after 2 years. Concentrations were raised less in the LF complex than they were after spring fertilization but H horizons were similarly affected (Tables 6-4 and 6-7). A major difference between seasons of application with respect to the disposition of ammonium occurred in the surface 20 cm of mineral soil. Concentrations during the first 6 months after fall fertilization were nearly double those seen during the same period following spring fertilization (Tables 6-4 and 6-7). This was approximately 72 kg ha^{-1} of additional available N at 3 weeks after fertilization (Fig. 6-3b). This difference in ammonium distribution can be explained by the lower temperatures and greater rainfall that followed fall fertilization (Table 6-3).

Recovery of N in inorganic forms for both chemical sources of N (Table 6-8) confirms that a fertilization effect on available N pools lasted 40 weeks at most. A disparity in recovery estimates by the difference and ^{15}N methods existed for urea-N, as had been the case after spring fertilization. Differences, though initially nearly double the magnitude after fall fertilization, were also short-lived. The amount of native ammonium in fertilized and control plots was not significantly different ($P=0.174$) at 28 weeks (Table 6-7).

Despite the greater mass of ammonium-N observed after fall-, as opposed to, spring-application of urea, immobilization rates were essentially the same (Table 6-6) and amount of fertilizer N immobilized at three weeks was greater in fall (Fig.6-4). An important difference, however, was that immobilization in fall was greater in mineral soil than forest floor whereas in spring the reverse was true. Penetration of fertilizer N to greater depth after fall fertilization was associated with reduced volatilization and increased the mineralization rate.

Although not statistically significant, there is a feature in the organic ^{15}N pattern that occurred in both seasons of application and is worthy of comment. It was observed

Table 6-7. Concentration of ammonium-N in forest floor and mineral soil after fertilization with urea and ammonium nitrate in fall.

Treatment	Weeks after Fertilization	LF	H	0-10 cm	10-20 cm	20-30 cm
		mg kg^{-1}				
Control	3	53.7 (10.9)	41.3 (5.8)	8.8 (0.8)	5.7 (0.1)	4.5 (0.5)
	13	73.3 (3.7)	41.3 (9.9)	8.8 (1.0)	6.4 (1.1)	4.7 (0.5)
	28	57.3 (8.2)	66.7 (24.7)	9.7 (0.2)	6.8 (0.8)	6.5 (0.7)
	40	47.3 (13.5)	47.7 (15.2)	9.4 (0.3)	8.2 (1.1)	6.3 (0.7)
	51	68.0 (28.8)	54.7 (11.2)	8.5 (0.9)	5.4 (0.2)	4.2 (0.8)
	102	61.3 (2.7)	36.0 (3.1)	6.5 (0.8)	4.2 (0.4)	3.2 (0.4)
AN	3	-	-	-	-	-
	13	-	-	-	-	-
	28	159.3 (16.1)	202.3 (29.1)	17.3 (0.6)	11.4 (1.8)	7.3 (1.4)
	40	-	-	-	-	-
	51	147 (3.0)	98.3 (3.3)	9.1 (0.3)	7.6 (1.2)	3.8 (0.2)
	102	54.7 (4.8)	37.3 (1.2)	6.9 (0.6)	4.2 (0.5)	3.1 (0.6)
Urea	3	1000 (79)	1440 (268)	235 (34)	67.0 (13.8)	25.9 (13.9)
	13	532 (9.2)	985 (250)	98.4 (19.9)	28.9 (10.1)	13.5 (4.3)
	28	261 (36.8)	307 (94.8)	35.0 (11.4)	12.1 (1.4)	8.4 (1.4)
	40	181 (18.2)	144 (9.6)	13.8 (1.2)	9.1 (0.6)	9.3 (2.2)
	51	246 (4.5)	146 (3.6)	10.1 (1.7)	6.2 (0.7)	4.6 (0.6)
	102	100 (11.7)	85.6 (16.0)	6.8 (0.7)	4.4 (0.5)	4.3 (0.7)

Table 6-8. Recovery of N in soil inorganic forms (SE) after fall fertilization of Douglas-fir with urea and AN @ 200 kg N ha^{-1}.

	Fertilizer Source			
	AN	Urea		
	Recovery, % of applied			
Weeks after Application	Difference Method		^{15}N Method	"Primed" NH_4^+-N, kg ha^{-1}
3	-	88.1 (19.6)	68.5 (7.3)	39.2
13	-	40.2 (9.5)	24.8 (3.4)	30.8
28	5.8 (7.4)	10.0 (6.5)	7.2 (1.8)	5.6
40	-	2.9 (2.1)	2.3 (0.5)	1.2
51	1.6 (3.3)	2.2 (1.4)	1.8 (0.2)	0.8
102	-0.6 (1.9)	0.2 (0.3)	0.9 (0.2)	-1.4

immobilized ^{15}N increased approximately 30 kg ha^{-1} from summer to late fall in the first year after fertilization (Fig. 6-4). In the case of spring fertilization there was sufficient ^{15}N-ammonium in mid-July of this year that the increase could have come from further immobilization (Table 6-5). However, after fall fertilization there was only about 6 kg ha^{-1} of ^{15}N remaining as ammonium at summer's end (Table 6-8). Therefore, the appearance of this amount of organic ^{15}N could not have come from microbial immobilization. A possible explanation lies in the production of fine roots by Douglas-fir. Coastal Douglas-fir routinely experience summer drought and root activity during this period is low (K. Vogt, pers. comm.). When soil moisture is replenished in fall a peak in root activity occurs. By this time internal pools of trees would be highly labelled irrespective of season of urea application (Chapter 5). Vogt et al. (1987) give typical fine root biomass for closed canopy Douglas-fir as 3,000 kg ha^{-1}. Assuming full replacement of fine roots 40% C by mass and having a C/N of 25, a requirement of 48 kg ha^{-1} of N may be calculated. The flux of 30 kg ha^{-1} ^{15}N therefore could have come from this process. This hypothesis could be falsified through analysis of fine roots in stored frozen samples.

Significance of Rate Estimates

It is important to distinguish rates derived from ^{15}N-enriched fertilizer experiments from those derived from physiological experiments. In the latter a small amount of highly labelled N is added in hopes that its introduction will not appreciably alter the natural cycling rates. Rates presented here represent only those of the perturbed system.

The rates of immobilization presented here are close to half that reported by Schimel and Firestone (1989) for forest floor slurries incubated at 20° C. Foster et al. (1985) and Schimel and Firestone (1989) both reported that a significant proportion of added ammoniacal N was immobilized by chemical means. This phenomenon may be more widespread than currently assumed. Very high *biological* immobilization rates are most easily understood when accompanied by a respiratory increase.

The difference in availability of ammonium at three weeks after spring and fall urea fertilization, approximately 70 kg N ha^{-1}, was not caused primarily by greater immobilization in spring (Table 6-6). Rather, higher volatilization and lower gross mineralization seemed responsible. Reasons for differences between seasons in volatilization rate have been discussed in detail (Chapter 3). Gross N mineralization was about 40 kg ha^{-1} greater after fall fertilization (Table 6-6), when labelled N was distributed more deeply than occurred after spring fertilization. This deeper penetration effectively reduced the urea-N concentration in any one horizon and should have limited the solubilization of organic matter owing to ureolysis. Several reports have noted that higher rates of urea addition were not as effective per unit N applied, in raising microbial respiration (Salonius 1972, Roberge 1976, Foster et al.1985). Foster et al. (1985) gave evidence that immobilization at high rates of N addition includes a significant contribution from chemical processes. Our results are in agreement with this hypothesis. Presumably organic matter solubilized under the influence of ureolytically-generated alkali is susceptible to microbial attack and would provide both a source of native N to be mineralized and a sink for ^{15}N. However, at microsites where pH rises much above neutral, rates of microbial activity may decline while rates of chemical reactions between ammoniacal N and organic matter increase (Nômmik and Vahtras 1982). Thus, when urea is confined largely to the forest floor as was the case after spring fertilization, the rate of N cycling through the microbial biomass may be less than when urea-N concentrations are reduced by redistribution through the mineral soil, as occurred in fall. These observations are also consistent with the difference in primed ammonium N (Fig. 6-3) seen between seasons of application: under the hypotheses of Jansson (1982) and Jenkinson et al. (1985) a greater "priming effect" or "added N interaction" seen after fall fertiilzation would be expected related to stronger biological immobilization.

Rates of N immobilization in forest soils remain a challenge to rationalize. Recently, Strader and Binkley (1989) reported complete immobilization within 1 day of addition of ammonium-N@ 50 mg kg^{-1} to surface soils from two low-productivity Douglas-fir ecosystems. These rates are well above those reported in the present work. Additional research is needed to clarify the nature of N immobilization in forest soils. In particular, an understanding of the partitioning of ammonium between chemical and biological fates is necessary, as well as information on the susceptibility to mineralization once immobilized. It appears from the present work that N immobilization cannot be fully understood from a standpoint of microbial requirements alone.

Dynamic Simulation of N Cycling

A simulation model was constructed to test the hypotheses concerning the movements and transformations of urea-N described above for the spring-fertilized case. The simulation was done with parsimony as the uppermost criterion. This meant that the only pools and processes originally in the model were those upon which unequivocal direct observations were made; viz. single, homogeneous pools represented by extractable ammonium and total Kjeldahl N; volatilization of ammonia, immobilization of inorganic N, and plant uptake. Implementation of additional pools and processes was done only when the existing model structure demonstrably failed to simulate the *behaviour* of the system. Once a minimum configuration for the model had been reached parameter estimates were generated by minimizing an objective function. The objective function was sum of the residual sum of squares over the selected normalized state variables (pools). Residual sums of squares were calculated from definition in a spreadsheet using tabular output from STELLA (High Performance Systems Ltd 1985) . This was an iterative process that involved primarily adjustment of rate parameters but also sizes of hypothetical, kinetically defined pools. The latter adjustments were the last to be made in an iterative sequence because starting variables were chosen to represent reasonable estimates based on literature from other soil systems and/or mass balance considerations.

Because ureolysis and volatilization had been shown to depend on microsite factors beyond the resolution of the soil measurements (Chapter 3), and taking into consideration that volatilization did not represent the principal fate of applied N, the volatilization process was treated as a simple, first order process that depended on ammonium mass in the LF and prevailed only for the first four weeks; the period over which the process was found, experimentally, to be active. The first order rate for the process was adjusted to yield the observed output of approximately 28 kg N ha^{-1} (Appendix 2). This resulted in slight overestimation of the amount of ^{15}N lost by this process since volatilized N was frequently lower in abundance than the extractable ammonium in surface horizons (Chapter 3). This was an approach clearly superior to optimizing mineralization-immobilization dynamics to produce soil ammonium of the same isotopic signature as the volatilized ammonium. It is, in fact, doubtful that such a scheme could be devised, were it sought.

Soil was treated as possessing only two layers: the LF complex, which lacked roots and was solely responsible for volatilization losses, and the aggregate of H horizon plus mineral soil to a depth of 30 cm. Plant uptake was restricted to this latter layer. This separation also grouped materials according to degree of humification. Ureolysis was assumed instantaneous in the LF and diffusion of ^{15}N from LF to the underlying layer was accomodated by a discontinuous, first order function of ammonium mass. The assumption of instantaneous ureolysis was not met because some residual urea was visible several days after fertilization (Chapter 3). This was not considered serious, however, because the period required for over 90% hydrolysis was likely a few days at most, a short period compared to the 105 week simulation. The existence of ^{15}N-urea was proxied by the differential mobility postulated for the ammonium ion, which was given a first order transfer coefficient of 0.6 wk^{-1} for the first two weeks but stepped to 0.055 wk^{-1} thereafter. This provided a rapid transfer of over half of the labelled N to underlying horizons within 3 weeks, as observed.

Immobilization and mineralization in both soil layers were treated as independent processes that were characterized by donor-controlled, first-order kinetics. These kinetic assumptions were designed to reflect the importance of diffusional constraints, which mimic first order processes at reaction surfaces (Engasser and Horvath 1973), on microbial activities. Mineralization kinetics have recently been described as either zero or first order (Myrold and Tiedje 1986, Seyfried and Rao 1988, Ellert and Bettany 1988). In some cases zero and first order models were equally satisfactory for a given soil (Myrold and Tiedje 1986, Seyfried and Rao 1988). This result is expected if mineralization occurs from a large pool which varies little in size. In the present work first order mineralization kinetics were assumed because the perturbation from fertilization would be expected to alter pool sizes.

The data did not fit well to a model comprised of only one type of organic N in each soil layer (Table 6-9). The lack of fit stemmed from a conflict between amounts and ^{15}N abundance of ammonium remineralized from organic matter. If mineralization rates were lowered sufficiently to account for the exponential decline in ammonium mass then the ^{15}N abundance remained much above the observed pattern. Conversely, if mineralization from a single pool was raised enough to dilute ^{15}N to the observed levels far too much ammonium was produced. This reciprocity was relieved to a large extent by the inclusion of two kinetically-distinct, independent, pools (Table 6-9). Ultimately, this arrangement also required modification for similar reasons.

Table 6-9. Residual sums of squares for three hypothetical models of soil N cycling after ^{15}N-urea fertilization of a Douglas-fir ecosystem.

	Residual Sum of Squares			
	-----LF horizons*-----		---H to 30 cm depth†---	
Model	Raw RSS¥	Scaled RSS	Raw RSS	Scaled RSS
Single Organic N compartment	2015	2.896	1759	3.462
Fast and Slow Organic N compartments	2534	2.226	2558	2.028
Above with stabilization from Fast to Slow	549	0.370	560	0.551

* Variables in objective function: mass of NH_4^+ in LF complex, ^{15}N abundance of NH_4^+ in LF complex, ^{15}N abundance of total Kjeldahl N in LF complex, $\Sigma^{15}N$ in LF complex, $\Sigma^{15}N$ in H to 30 cm depth layer.

† Variables in objective function: mass of NH_4^+ in H to 30 cm depth layer, ^{15}N abundance of NH_4^+ in H to 30 cm depth layer, ^{15}N abundance of total Kjeldahl N in H to 30 cm depth layer, $\Sigma^{15}N$ in H to 30 cm depth layer.

¥ RSS = residual sum of squares

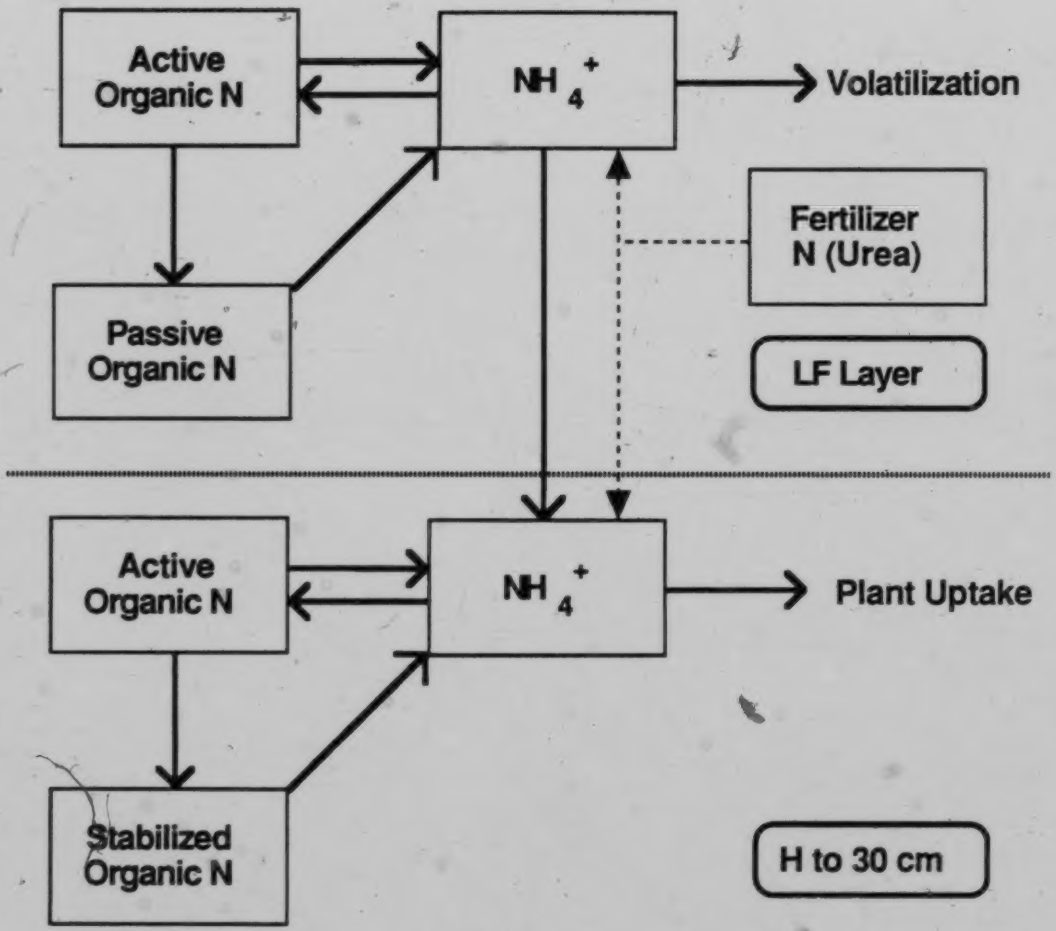
Active Organic N
NH $_4^+$
Volatilization
Passive Organic N
Fertilizer N (Urea)
LF Layer
Active Organic N
NH $_4^+$
Plant Uptake
Stabilized Organic N
H to 30 cm

Figure 6-8. Model used to describe N cycling in first year after fertilization of a forest soil with ^{15}N-labelled urea @200 kg N ha^{-1}. Because observations on soil pools began after ureolysis was complete, fertilizer N is represented initially through NH_4^+ pools.

Linking the two pools of organic N via an irreversible flow proved to be the arrangement which best described the data (Fig. 6-8). This irreversible pathway has been interpreted in agricultural and grassland systems (McGill et al. 1981, Juma and Paul 1981) as stabilization of organic N, by physical or chemical means, against microbial attack. Physical protection of organic matter in the current study could not have relied on phyllosilicate clay minerals as suggested by McGill et al. (1981) because the very small amounts of phyllosilicate clay present were low in both charge and specific surface. Amorphous colloidal materials, characteristic of podzolic soils, have recently been described as conferring similar stabilization on N in tephra-derived soils of France (Boudot et al. 1988). Stabilization of N in mineral horizons in the present work may have been by this mechanism but forest floor kinetics require an alternative interpretation. A more plausible connection between the modelled kinetic fractions and the physico-chemical state of forest floor materials is that the high turnover fraction represents N associated with biomass and easily-degraded residues such as proteins, aminopolysaccharides and other metabolically important compounds; whereas N in the slower turnover fraction might consist of structural components of the litter.

As currently structured, the model provides for immobilization only into the high turnover pools with subsequent stabilization into the slower pools. This structure was chosen to represent immobilization as proceeding through microorganisms only. However, it was not possible to get a good fit to the data with a single immobilizaton rate. Immobilization during the first few weeks was extremely rapid and could not be accomodated by a rate constant compatible with turnover patterns later in the experiment. Trebling the rate constant for the first two weeks (Appendix 2) took into account the increase in organic matter availability expected from ureolysis but may simultaneously have described chemical immobilization processes peculiar to high pH conditions.

Output of the model is plotted alongside experimental data in Fig. 6-9. Overall, the fit of the data to the model was quite good, generally, variables were predicted within experimental error. The main exception to this was the mass of ammonium in the H to 30 cm layer in the later stages of the experiment. The model underestimated this variable by approximately 6 and 15 kg ha^{-1} at 54 and 105 weeks, respectively. This was probably related to a lack in the model of fresh plant residues, perhaps fine roots in particular. Consistent with this explanation is the underestimation of the ^{15}N enrichment of total Kjeldahl N in the H to 30 cm layer from 28 to 54 weeks.

The model (Fig. 6-8) was synthesized from data collected after fertilization in spring. Since transport and volatilization rate parameters were empirically derived, but ultimately were functions primarily of unmeasured soil moisture and thermal fluxes, it is not expected that the model would accurately simulate behaviour after fall fertilization. However, allowing for empirical parameterization of urea-N transport in fall, the microbial- and plant-based parameters could be tested. Coefficients for processes such as immobilization and plant uptake will show temperature dependence, and temperature differences existed between spring and fall; but they may respond in parallel (i.e. have the same Q10 coefficients) and still permit validation of the model structure.

Summary and Conclusions

Nitrogen from fertilizers applied in spring and fall to a skeletal, podzolic forest soil supporting the growth of a 38-year-old, second growth stand of Douglas-fir was strongly retained in the soil-plant system. At the end of 2 years soil recovery of urea-^{15}N was estimated at 50 to 57% for spring and fall applications, respectively. Availability of N was very high initially but declined exponentially such that 6 months after fertilization only about 5-10% of applied N remained in inorganic forms. By following the movement of ^{15}N it was shown that the major fates of applied urea-N were immobilization, plant uptake, and volatilization. Nitrification and denitrification did not appear to play a major role.

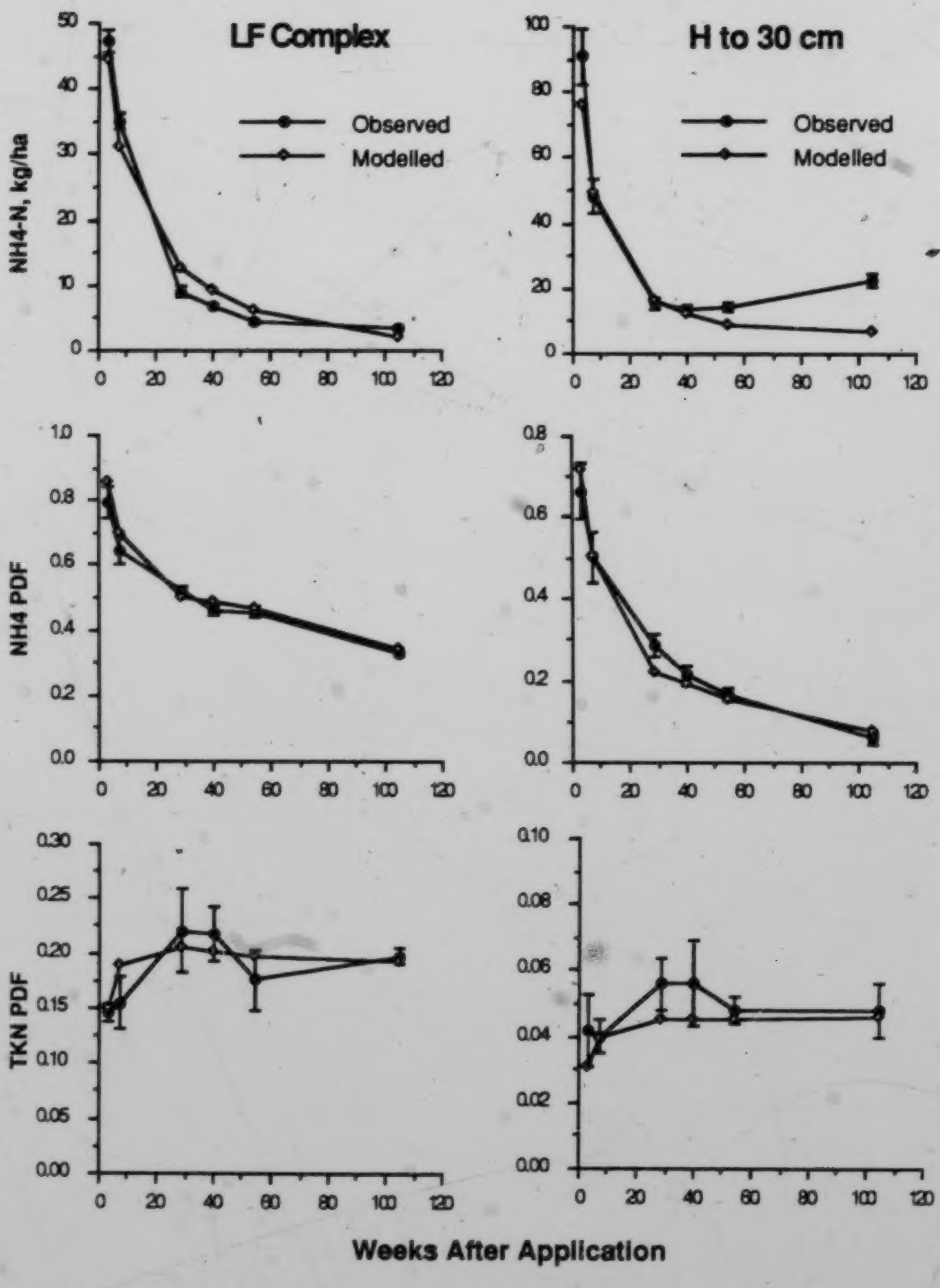

Figure 6-9. Observed and modelled N variables in soil fertilized in spring @ 200 kg ha-1 as urea. One arm of an error bar equals standard error of mean of three plots. PDF = proportion due to fertilizer, TKN = total Kjeldahl N.

Immobilization of urea-N was very rapid in the forest floor and surface mineral soil irrespective of season of application. Gross mineralization was lower, and volatilization higher, in the first 3 weeks after spring fertilization. Differences in the rates of these processes between seasons of application appeared to be related to the vertical distribution of applied N, which was largely a function of post-fertilization rainfall. It was hypothesized that confinement of urea to forest floor materials, as occurred in spring, favoured chemical reactions between ureolytic products and organic matter, which yielded organic N less disposed towards short-term mineralization than N that had been biologically immobilized. Despite the fact that mineral N levels had returned to near control levels within a year of treatment, ammonium pools continued to be much more highly labelled than the presumed organic matter source. This suggested that organic matter was not homogeneous and the majority of recently added N was cycling through a subcompartment. Abrupt changes in amounts of Kjeldahl N seen in this study may represent an important, essentially uncharacterized, N subcycle from fine roots to soil.

A simulation model of N transformations and transfers was constructed using data from the spring urea treatment. The model described N cycling in both the forest floor and mineral soil as occurring among two kinetically-defined organic pools and ammonium. Kinetics were treated as first-order and donor-controlled. The model explained fairly accurately the amount and ^{15}N abundance of ammonium as well as the ^{15}N abundance of the total organic matter during the first year after fertilization. In the second year few data were available but it appeared that the model broke down due to the lack of treatment of N-return from trees to soil.

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7. GROWTH RESPONSE OF DOUGLAS-FIR TO SPRING AND FALL APPLICATION OF AMMONIUM NITRATE AND ^{15}N-UREA AND ABOVEGROUND RECOVERY OF ^{15}N AFTER THREE GROWING SEASONS

7.1 Introduction

Coastal Douglas-fir stands often respond positively to additions of N (Heilman and Gessel 1963). Operational N fertilization of Douglas-fir has been sporadic since the late 1960's but probably will become more common as demand for forest products rises in relation to allowable cuts. Traditionally, urea has been used as the chemical source of N but some recent reports (Harrington and Miller 1979, Dangerfield and Brix 1981, Barclay and Brix 1984) have shown better response to ammonium nitrate (AN). AN is the preferred N source in Scandinavian forestry (Malm and Möller 1975) but has been used sparingly in North America because of its lower N analysis than urea, and certain difficulties in its handling related to its oxidizing potential. In addition, a number of studies have indicated no significant difference in growth response to the two sources.

It has been suggested that differences in N availability between the two sources arise primarily from the degree of immobilization occurring immediately after application and that this is accentuated in cold soils with deep forest floors (Bengtson and Kilmer 1975). Other potential sources of variation include differences in leachability (Overrein 1968) and susceptibility to volatilization (Watkins et al. 1972). All of these processes are subject to modification by weather patterns and thus, different season of application for fertilizers may present opportunities for optimizing N efficiency.

Studies investigating chemical source of N and season of application have usually been carried out under conditions that do not approximate a typical management scenario. For example, AN experiments at Shawnigan Lake, B.C. (Barclay and Brix 1984) and

Wind River, WA (Miller and Tarrant 1983) were both in very low productivity systems. Heilman et al. (1982) compared spring and fall urea applications to Douglas-fir on high site land but the trees used were only 7 and 9 years old. Harrington and Miller (1979) compared urea and AN sources directly but this was in a 110-year-old stand - much older than would normally be considered for operational fertilization.

The present work reports on aboveground growth responses and fertilizer recovery as part of a larger N cycling study that compared the effects of urea and AN fertilization in spring and fall in a Douglas-fir stand representative of a high priority candidate for fertilization.

7.2 Materials and Methods

Study Site and Experimental Design

The study site and experimental design are described in detail in Chapter 2.

Stand Sampling and Mensuration

Height, by clinometer, and breast height diameter (dbh), by diameter tape, of all trees were measured before treatment and after three growing seasons (Table 7-1). In late August 1985 three trees selected to represent dominant/codominant (two) and intermediate crown classes (one) were selected in all control and fall urea-fertilized plots for more detailed growth analysis and analysis of ^{15}N abundance. Diameter of the bole, and two increment cores, oriented 90

Table 7-1. Timetable for mensuration.

Season of Application	Initial	Final
Spring	May 2-5, 1982	August 22-24, 1984
Fall	October 15-18, 1982	August 25-28, 1985

degrees to one another, were taken at the base and midpoint of the live crown. On urea-fertilized trees two branches were removed from each of the 6th whorl, mid-crown, and lowermost whorl possessing at least 5 age classes of foliage. The diameter, proximal to the bole, and total length of each branch were measured. The laterals and axial material up to age 5 were removed from each branch and the remaining material cut into lengths, dried at 70 °C, and weighed and bulked for ^{15}N analysis using subsamples proportional to dry mass. Branch material 4 years of age and younger was segregated into needles and branchlets of equal age. Remaining materials ≥ 5 yr old were grouped within tissue type (branch or needle). All components were dried at 70 °C, weighed, and analyzed for N concentration and ^{15}N abundance, described below.

Laboratory Analysis

Annual radial growth was determined from increment cores with aid of a computer-assisted measurement system (Clyde and Titus 1987). Samples for ^{15}N analysis were broken up in a large Wiley mill, then ground in a reciprocating ball mill to pass a 60 mesh sieve. Nitrogen concentrations and ^{15}N abundance were determined using a Dumas-based Carlo-Erba gas analyzer coupled to a VG-Isogas automated, ratio mass spectrometer.

Data Analysis

Only trees within 5 m of plot center were used in the analyses. These "inner plot" trees comprised 65% of experimental trees and had previously been shown (Chapter 5) to be essentially free of edge effects. Volume growth response was calculated using the regional equations of Bruce and DeMars (1974). Masses of components were estimated using the log-log regressions of Grier et al. (1984) after correction for bias as suggested by Baskerville (1972). Initial height, basal area projected from breast height, and volume varied among plots (Chapter 2). Preliminary analyses showed that growth was highly correlated to initial tree dimensions and, therefore, these were used as covariates in statistical comparisons (Woolons and Whyte 1988), pairing the dimension to its corresponding growth estimate. Analyses of height growth were performed on arithmetic means for plots. Mass, basal area and volume growth analyses were performed on plot values obtained by calculating these variables for each tree, summing over all trees in the inner plot, and dividing the result by the inner plot area.

Data were analyzed as a two-way analysis of covariance with season of application (2 levels) and fertilizer treatment (3 levels) as grouping factors and the appropriate initial dimension as the covariate. All computations were done in the MGLH module of SYSTAT (Systat Inc. 1986). Means presented in tables and figures are adjusted for the effect of the covariate unless otherwise specified.

A total fertilizer N uptake into crowns was calculated by pooling N concentration and ^{15}N abundance data across all nine study trees to obtain weighted means which were then input to the regressions of Grier et al. (1984). For this procedure the actual stocking levels of the inner plots were used to compute a mean dbh from the basal area in the plots.

7.3 Results and Discussion

Growth Response

Height growth of all trees differed between the two three-year periods examined (Table 7-2), averaging 1.92 and 1.27 m after spring and fall treatments, respectively. Fertilizer treatment was not significantly different (P=0.135, Table 7-2) despite increments over control as high as 58% (Fig. 7-1). Height increments were greater after fertilization with AN than was the case for urea. Urea applied in fall appeared to depress height growth somewhat although the difference was not significant. The difference in height growth between seasons was unexpected and difficult to explain. The majority of the difference stems from the strong growth response seen in the AN treatment but both controls and urea-fertilized trees grew more in height also. A possible explanation lies in the rainfall patterns in the second growing season after fertilization. Because growth in Douglas-fir is

Table 7-2. Covariance-adjusted estimates of Douglas-fir growth over three growing seasons after spring- and fall-fertilization with N @ 200 kg ha^{-1} as ammonium nitrate (AN) or urea.

Estimate of Growth	Control	AN	Urea
		Spring	
Height, m	1.51	2.36	1.88
Basal Area, m^2 ha^{-1}	3.58	5.48	4.23
Volume, m^3 ha^{-1}*	61.4	97.1	68.7
Aboveground Biomass, Mg ha^{-1}†	22.2	33.5	26.1
		Fall	
Height, m	1.25	1.45	1.13
Basal Area, m^2 ha^{-1}	3.59	5.58	4.76
Volume, m^3 ha^{-1}	56.1	73.8	54.9
Aboveground Biomass, Mg ha^{-1}	22.1	34.7	29.4

Summary of ANCOVAR¥, probability level of F statistic

Source of Variation	Height Growth	Basal Area Growth	Volume Growth	Biomass Growth
Season of Application	0.009	0.507	0.038	0.450
Treatment	0.135	0.001	0.006	0.001
Season x Treatment	0.424	0.768	0.479	0.767
Covariate	0.001	<0.001	<0.001	<0.001

* Based on equations of Bruce and DeMars (1974)

† Based on equations of Grier et al. (1984)

¥ n=3

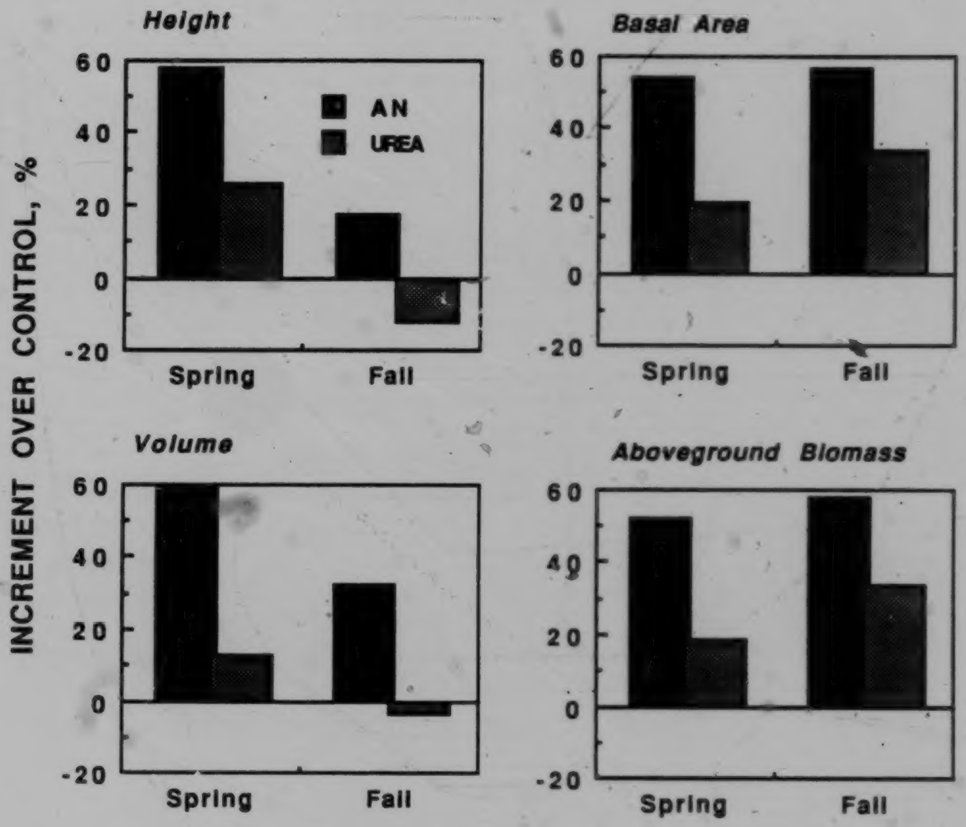

Figure 7-1. Three-year stand growth response of 38-year-old Douglas-fir to N fertilization @ 200 kg ha^{-1} ammonium nitrate (AN) or urea in spring and fall.

determinate (Allen and Owens 1972) a height growth response in the first year after fertilization is constrained. The maximum response would be expected in the second year, 1983 and 1984 for spring- and fall-fertilized trees, respectively. Late spring and early summer, the period in this region for Douglas-fir shoot extension, was wetter in 1983 than in 1984. Throughfall for the period May 15 to July 15 totalled 17 cm in 1983 whereas the total in 1984 was 8 cm. Presumably, the amount of water available during shoot elongation will influence the total extension achieved.

Generally, height growth has not been as greatly affected as diameter growth by addition of limiting nutrients (Bevege 1984). Nambiar and Bowen (1986) reported no effect of fertilization on height growth of radiata pine whereas a 27% increase in biomass was observed. Low site quality Douglas-fir responded to N fertilization by increasing height growth by 30 to 40% over a 9 year period (Barclay et al. 1982). Another study on a low productivity Douglas-fir site in Washington yielded height growth increases of approximately 30% over 15 years from a single application of AN @ 157 kg N ha^{-1} (Miller and Tarrant 1983). The height responses recorded after spring fertilization in the present study are thus comparable to other estimates for Douglas-fir but the fall height growth response seems anomalously low.

Basal area growth was strongly affected by fertilization (Table 7-2). Ammonium nitrate elevated basal area growth by about 54% irrespective of season of application (Fig. 7-1) whereas urea fertilization was followed by an average increase of 25%. Greater basal area growth in Douglas-fir from AN, as compared to urea, has been reported by Harrington and Miller (1979), Dangerfield and Brix (1981), and Barclay and Brix (1984). The current study augments these findings and tends to suggest that Douglas-fir systems in the Pacific Northwest behave with greater similarity to Scandinavian coniferous systems, where the superiority of AN is now well established, than to southeastern USA pine systems, where AN and urea generally give similar results (Pritchett and Fisher 1987).

Volume growth response differed in both season of application and with respect to fertilizer treatment (Table 7-2). Ammonium nitrate gave an average increment over control of 45% whereas urea fertilization resulted in an average of only 5%. This low estimate was influenced primarily by the lower height increment in trees fertilized in fall with urea; that is, the volume equation of Bruce and DeMars (1974) was very sensitive to height. By contrast, the estimates of aboveground biomass increment (Table 7-2, Fig. 7-1) showed fall application of urea to increase growth by about 30% over control. Volume and aboveground biomass growth responses would, barring large changes in density of tree components, be expected to show parallel trends. Estimates of aboveground biomass were generated with regressions based on breast height diameter only (Grier et al. 1984). In their study, only the allometry between dbh and current twig and foliage mass was altered by fertilization. Similarly, Thomson and Barclay (1984) found that radial growth pattern along the bole was not significantly altered by fertilization. In our study fall urea fertilization differentially promoted diameter over height growth, an apparent anomaly.

Radial growth response at three positions on the bole was analyzed as a split-split plot with fertilizer treatment in the main plot and height and year in the split plots (Table 7-3). No pretreatment differences existed between treatments for this variable so data were analyzed without a covariate. A significant treatment by year interaction showed that enhancement of radial growth had taken place (Table 7-3). Increments in the upper bole appeared to be greater than at breast height (Fig. 7-2) but the treatment by height interaction was not significant. It was notable that the increment at the mid-crown position in 1984 showed a peak in control trees but not in urea-fertilized trees. This is the same year that had poor water availability during the shoot elongation phase.

Table 7-3. ANOVA for annual radial growth in Douglas-fir

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	P
Treatment ,T	1	9.624	9.624	2.076	0.2230
Plots, P within treatment , P/T (Error 1)	4	18.540	4.635		
Year, Y	3	8.052	2.684	19.087	0.0001
YT	3	1.699	0.566	4.027	0.0339
YT x P/T (Error 2)	12	1.687	0.141		
Height, H	2	44.729	22.364	54.731	0.0000
HT	2	0.144	0.072	0.176	0.8414
HT x P/T (Error 3)	8	3.269	0.409		
HY	6	1.021	0.170	1.923	0.1181
HYT	6	1.129	0.188	2.125	0.0875
HYT x P/T (Error 4)	24	2.124	0.089		

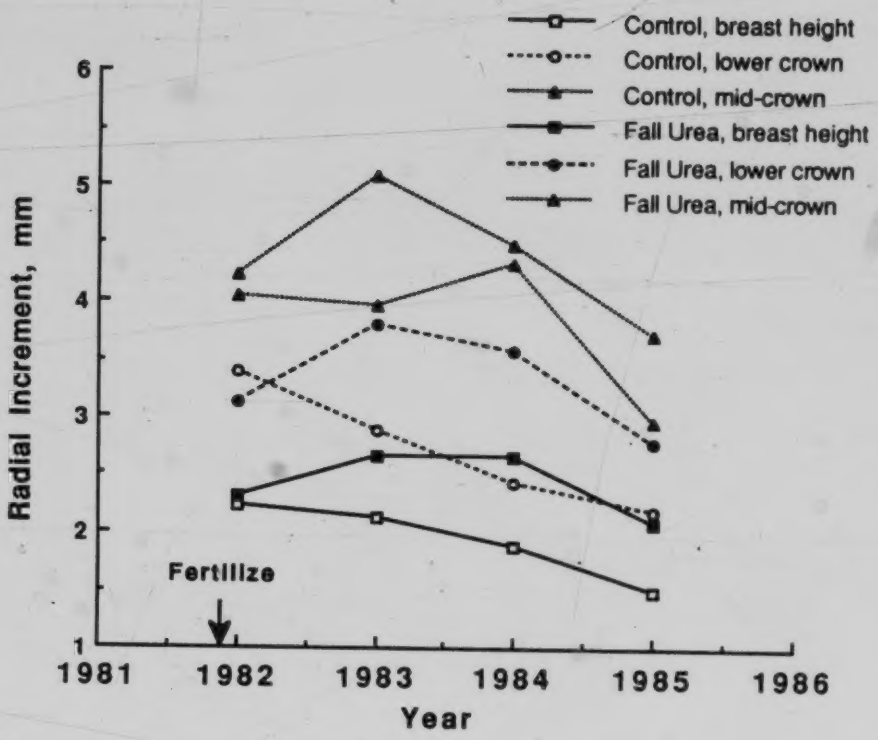

Figure 7-2. Annual radial increment of Douglas-fir boles at three crown heights after fall fertilization with N@ 200 kg ha^{-1} as urea.

Disposition of ^{15}N in Trees After Three Growing Seasons

Urea-N was heterogeneously distributed among branch and foliar components (Figs. 7-3 and 7-4). Greater ^{15}N enrichments were recorded in the upper portion of the crown for both branches and foliage. These higher enrichments in mid- to upper-crown are consistent with a higher photosynthetic rate (Brix 1981) and, therefore, N demand found in this zone of the canopy. Enrichment of ^{15}N declined from newer to older tissues with the exception of the oldest class, which grouped all materials $\geq$ 5 years old (Fig. 7-3). Approximately 25% of the branch biomass for the crown heights sampled was in this age class, which represented the large diameter portion proximal to the bole. The higher ^{15}N enrichment may reflect metabolic activity associated with secondary thickening necessary to support an increased foliar biomass. Overall, however, the highest ^{15}N enrichments occurred in branch tissues formed after fertilization. The level of ^{15}N enrichment in branches, approximately 75% of that recorded in needles is, surprisingly high in view of the high proportion of structural tissue in the former. These enrichments may be understood, however, if N is concentrated in non-structural tissues. Concentrations of N in branches were low (Table 7-4) but likely concentrated in the cambium where metabolic activity is high.

Nitrogen in current and one-year-old foliage in the mid- to upper-crown was enriched in ^{15}N at a level very close to peak levels seen one year after fertilization (cf. Fig. 5-3b). This may reflect partly the fact that fewer trees could be sampled in detail at the end of the study and some upward bias may have been introduced. Nevertheless, the high proportion of fertilizer N in the needles exceeded that in soil ammonium pools at 2 years (Chapter 6) and clearly indicates that N was being actively recycled within the trees.

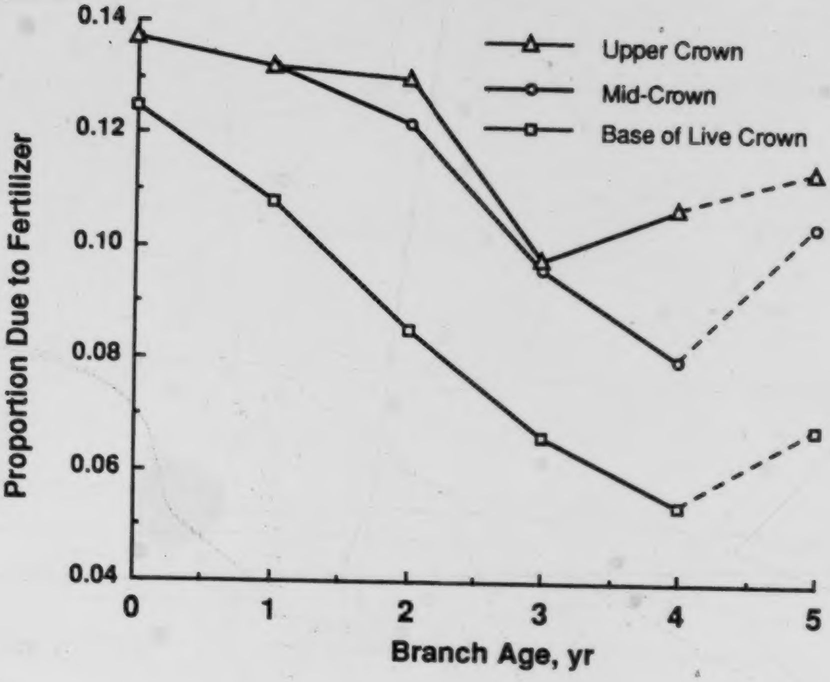

Figure 7-3. Distribution of fertilizer N in branches at 3 crown heights in Douglas-fir after fall fertilization with ^{15}N urea @ 200 kg ha^{-1}. Tissue age 5 includes all branch material greater than 5 years age.

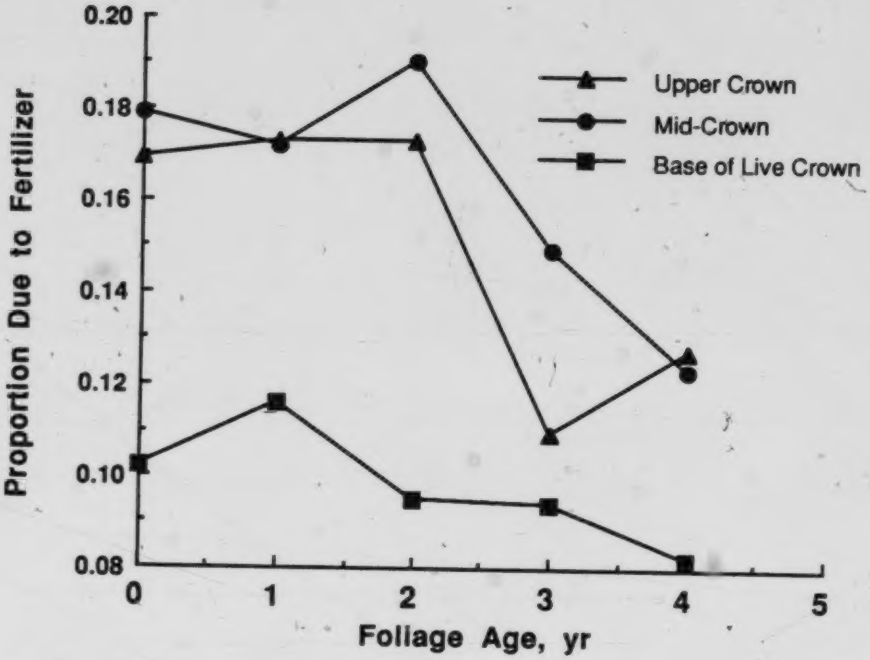

Figure 7-4. Distribution of fertilizer N in foliage at 3 crown heights in Douglas-fir after fall fertilization with ^{15}N-urea @ 200 kg ha^{-1}.

Table 7-4. Concentration of N in branch and foliage cohorts of Douglas-fir three growing seasons after fall fertilization with urea. n=9 trees.

Crown Position	Age	Branches		Foliage	
		%N	(SE)	%N	(SE)
Upper crown	1985	0.79	0.04	1.13	0.08
	1984	0.53	0.02	1.10	0.03
	1983	0.51	0.06	1.24	0.06
	1982	0.45	0.01	1.23	0.04
	1981	0.55	0.10	1.13	0.11
	1980	0.27	0.01	-	-
Mid-crown	1985	0.61	0.10	0.94	0.06
	1984	0.49	0.06	1.06	0.02
	1983	0.46	0.04	1.10	0.08
	1982	0.49	0.01	1.04	0.08
	1981	0.52	0.09	0.95	0.05
	1980*	0.21	0.01	-	-
Base of live crown	1985	0.64	0.05	0.91	0.02
	1984	0.58	0.03	0.95	0.05
	1983	0.55	0.03	1.00	0.06
	1982	0.51	0.01	1.01	0.10
	1981	0.42	0.02	0.93	0.09
	1980*	0.18	0.01	-	-

* includes tissues older than 1980, as discussed in Materials and Methods.

Our estimate of fertilizer N in crowns at three years was 35 and 11 kg ha^{-1} in foliage and branches respectively, about the same amount as had been estimated in foliage and twigs at 2 years after fertilization (Chapter 5). The total of 46 kg ha^{-1} is equivalent to a 23% recovery. This is slightly below the 25 to 36% reported by Heilman et al. (1982) for 7 and 9 year-old Douglas-fir but our estimate does not include N in bole tissues. Other estimates of fertilizer efficiency in coniferous systems are lower. Nambiar and Bowen (1986) found 18% of applied $^{15}(NH_4)_2SO_4$-N in young radiata pine after 4 years, whereas Mead and Pritchett (1975) recovered only 11% of $^{15}(NH_4)_2SO_4$-N applied to slash pine. On the other hand, Melin and Nômmik (1988) reported 44% recovery after 2 years of ^{15}N applied as $Ca(NO_3)_2$ and 30-33% recovery applied as urea to Scots pine and Norway spruce. In the latter study urea fertilization resulted in 30 to 33% recovery in trees. It was reported also that approximately 25% of recovered N resided in bole wood and bark. If a similar proportion was allocated to boles in the present study fertilizer recovery would be near 31% of applied.

Our estimate of recovery, and all others mentioned above, assumes that fertilizer N mixes instantaneously with available soil N. This assumption is demonstrably violated by the mineralization-immobilization turnover occurring in soil and must result in underestimation of uptake (Jenkinson et al. 1985). Alternatives to the static dilution approach to fertilizer uptake were examined in Chapter 5.

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8. SYNTHESIS

In this study forest N cycling patterns were both manipulated and probed by the addition of relatively large amounts of chemical fertilizers: AN and ^{15}N-urea. The dominating characteristic of the Douglas-fir system observed was the tight conservation of added N, irrespective of chemical source. Retention of N resulted from chemical and biological processes that frequently interacted. The principal processes accompanying applications of urea were immobilization, and secondarily, plant uptake. The balance between these two was altered by weather patterns, particularly rainfall. The fate of ammonium nitrate was not known to the same level as for urea because no tracer N was included in this source and soil sampling was less frequent. Plant analyses, however, suggested that this form of N was more available to Douglas-fir. Growth performance of Douglas-fir was consistent with the hypothesis, based on foliar analyses, of N limitation.

Urea labelled with the stable isotope ^{15}N permitted quantification of the fate of added N. Rates of plant uptake, immobilization, and mineralization of N could be estimated over certain periods. The estimation of rates by dilution methods (Jacquez 1972) was frequently hampered by the general absence of steady state conditions in the system. Ultimately, the best way to describe N cycling was through the construction of a simulation model based on ^{15}N kinetics (Figure 8-1). The central concept of the model is multiple pools of kinetically homogeneous N both in the soil and plant. These pools were invoked only when simulation using a single, homogeneous pool failed to adequately describe the data. Details of the processes and concepts outlined above follow.

Fate of Urea in Soil

Urea applied to forest soils is rapidly hydrolyzed by high levels of urease (Roberge and Knowles 1966) as was the case here. Ureolysis is an alkalizing reaction, however, and the fate of the released ammonium is dependent upon the degree to which reaction

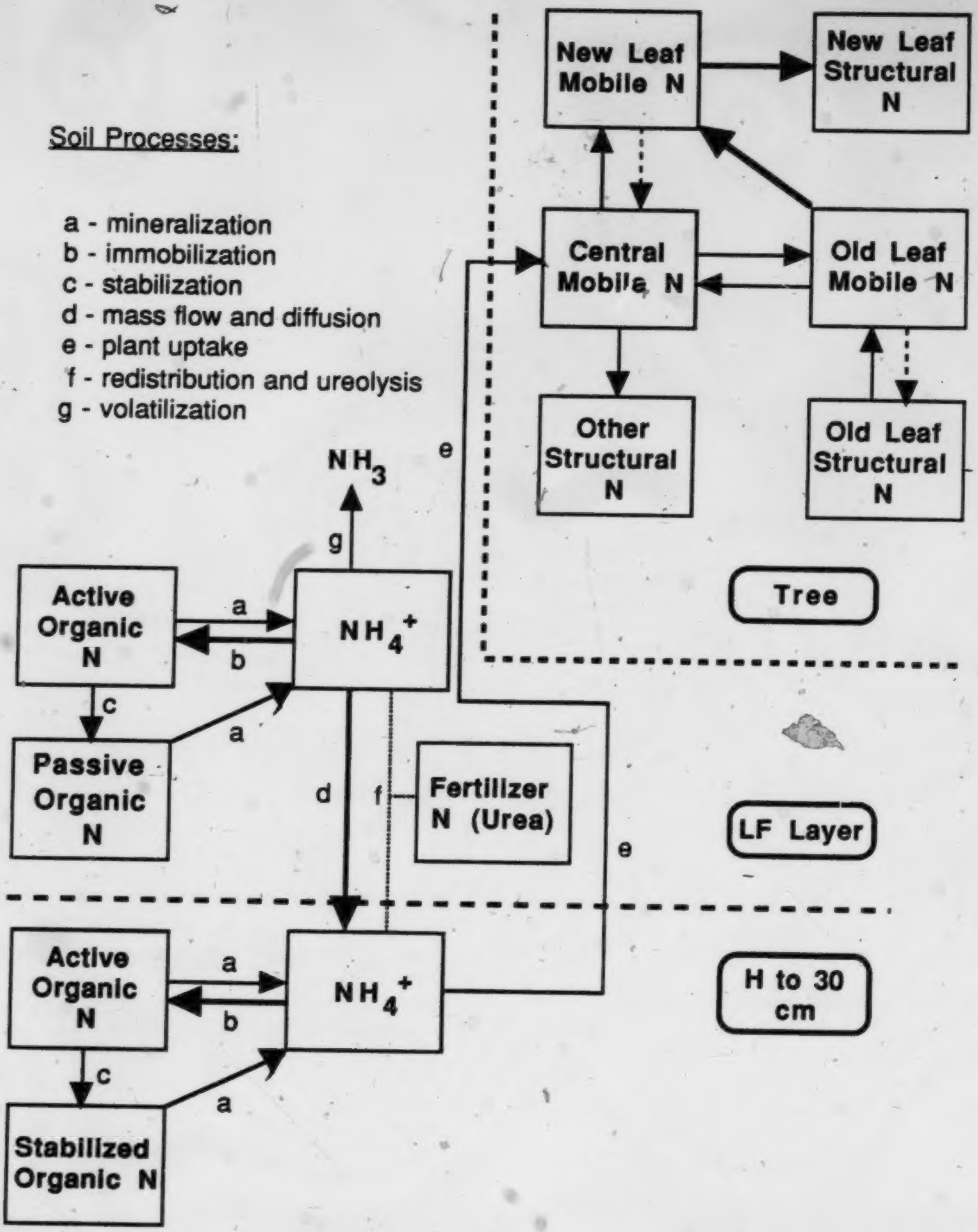
Soil Processes:
a - mineralization
b - immobilization
c - stabilization
d - mass flow and diffusion
e - plant uptake
f - redistribution and ureolysis
g - volatilization
New Leaf Mobile N
New Leaf Structural N
Central Mobile N
Old Leaf Mobile N
Other Structural N
Old Leaf Structural N
Tree
NH3
g
e
Active Organic N
NH4+
a
b
c
a
Passive Organic N
d
f
Fertilizer N (Urea)
e
LF Layer
Active Organic N
NH4+
a
b
c
a
Stabilized Organic N
H to 30 cm

Figure 8-1. Simulation model of N cycling in a Douglas-fir ecosystem fertilized in spring with ^{15}N urea. Within soil or tree, fluxes ranked by arrow weight.

products are dispersed and buffered (Rachhpal-Singh and Nye 1984). Under the dry, warm conditions that prevailed after spring fertilization, dispersion of alkalinity was restricted and ammonia was volatilized from the forest floor. About 28 kg N ha^{-1} was evolved, approximately 60% of fertilizer origin. It was noted that volatilized N did not match the ^{15}N abundance of KCl-extractable soil N which lead to the conclusion that ammonia was leaving from microsites isolated from the "bulk soil solution".

Volatilized ammonia is not necessarily lost from a Douglas-fir system. Potted Douglas-fir seedlings positioned above the forest floor captured easily-detected amounts of tracer N. The amount captured suggested that between 10 and 20% of volatilized ammonia could be captured by a plant canopy at approximately 25 cm elevation. Amounts captured by seedlings at 150 cm elevation were a small fraction of this amount and indicated that the plant recapture mechanism would most likely benefit understory species.

Very little ammonia evolved when urea was applied in fall. Heavy rainfall before and after fertilization served to disperse urea and its hydrolytic products.

Urea-N penetrated to below 20 cm within 3 weeks irrespective of season of application. As essentially no leaching occurred after spring application N movement was mainly diffusional and therefore based on movement of complexes of low charge - perhaps organic forms. Roughly half of the soil ^{15}N recovered at 3 weeks was already in organic forms indicating rapid immobilization processes. A greater proportion of fertilizer N and higher amounts of available N were found in the A horizon after fall fertilization.

Inorganic N was dominantly ammonium ion. Nitrate-N only once rose above 2 mg kg^{-1} soil. Ammonium levels of urea-fertilized plots were drastically elevated for the first few weeks but declined exponentially throughout the first year. After 6 months NH_4^+ concentrations in mineral soil and forest floor were about 4-5 times that of control. Longer and greater enhancements resulted from application of urea in fall vs spring. The ephemeral improvement in soil ammonium concentrations suggested plant uptake would be increased mainly in the first few months only.

Rates of immobilization could not be calculated directly from the data after 3 weeks had elapsed because no consistent trend in ^{15}N abundance of organic N was evident. Immobilization rates during the first 3 weeks were approximately 45 kg ha^{-1} wk^{-1} regardless of the season of application. The anticipated explanation for differences in urea-N availability between seasons was variations in the immobilization rate, controlled by soil temperature.

Gross mineralization values during the first three weeks when plant uptake was measured, and leaching assumed negligible, suggested concurrent rate of mineralization rather than rate of immobilization as the reason for differing availabilities of N in the two seasons of application. There are at least two explanations for this pattern. First, slow mineralization might reflect a seasonally-variable microbial use of wide C/N substrates that raise microbial demand for exogenous N. Second, recently immobilized N after spring fertilization may be less mineralizable than that immobilized after fall fertilization. Literature evidence suggests the latter is more likely. Salonius and Mahendrappa (1979), Foster et al. (1985), and Nômmik and Vahtras (1982) have shown that high pH accompanying ureolysis can promote chemical reactions between ammoniacal N and organic matter. Since these reactions are not under biological control there is little reason to believe that chemical bonds formed will be easily degraded by soil microbes, which have evolved enzymatic apparati for coping with biologically-generated substrates. It is thus proposed that both biological (plant uptake, microbial immobilization) and chemical feedback mechanisms operated to depress soil ammonium levels after urea fertilization.

Application of urea and AN to Douglas-fir in spring and fall resulted in pronounced differences in the behavior of urea-N but not AN-N. AN generally gave stronger responses in foliar N status and subsequent growth response. Volatilization and gross mineralization after urea fertilization were seasonally dependent and tied to weather-induced alterations to the chemical reactivity of urea and its hydrolytic products. In particular, high temperatures and constrained movement of urea after spring fertilization resulted in volatilization of ammonia and reduced gross mineralization. Reduction in mineralization rate was thought to be caused by chemical side reactions of ammoniacal N with soil organic matter.

The State of Organic N in Soil

The complexity of N transformations in soil lead to the development of a simulation model (Chapter 6, Figure 6-8) to test hypotheses. As anticipated N dynamics could not be described well with a single pool of organic N. The persistence of the ammonium pool at labelling intensities far above those of the total soil organic matter indicated that an actively recycling fraction must have existed. The data were best described when the active fraction was set at about 30% of the total organic N. It is difficult, if not impossible, in the present work to correlate this N with any particular physical, biological or chemical grouping because horizons containing disparate amounts and qualities of organic matter had to be pooled for the analysis. It is probable, however, the active fraction would contain the soil microbiota and recent metabolites. The passive N fraction may contain more of the organic constituents that are characterized as chemically amorphous and/or polydisperse, i.e. the humic substances, as well as N protected from mineralization by physical means.

An important feature of our model is that an irreversible flow is postulated between active and passive organic N, i.e. *stabilization* of organic N occurs. Models evolved from grassland systems (e.g. McGill et al. 1981) have provided for stabilization of organic matter in association with clay minerals. Such a mechanism is unlikely here because the fine earth fraction was < 3% clay, the majority of which was chlorite (Chapter 6). Amorphous constituents characteristic of podzolization processes (Boudot et al. 1988) are more likely to have played a role here.

Soil N cycling was treated as occurring among three pools: ammonium ion, and slow- and fast-turnover pools of organic N. Stabilization of fast-turnover organic N was the mechanism for the production of slow-turnover N. This mechanism was suggested to be mediated by amorphous constituents characteristic of the podzolization process.

Models of the soil N cycle are abundant for agricultural and grassland systems. Little has been done in attempting a simulation of forest N cycling on a short-term basis, however. Our model may serve as a point of departure for future, more robust, descriptions.

Plant Uptake

Declines in ^{15}N in soil were largely countered by plant uptake throughout the first year after fertilization. A quantitative estimate of uptake rate was permitted by use of simultaneous equations describing the decline in ammonium enrichment concurrent with accumulation in older foliage. This procedure indicated uptake was occurring at nearly twice the rate for the first few months after fall, as opposed to spring, urea fertilization. The method assumed that the principal site for N accumulation was the foliage and not some component that was not measured. Clearly, N passes first through roots and xylem tissues in transit to foliage. This was compensated for by introducing a lag in the estimation function. Ideally, the size and ^{15}N abundance of these intervening components should be measured. Attempts to have these parameters estimated by nonlinear regression coupled to a numerical integration scheme failed to converge (Statistical Consultants Inc. 1985). The lack of convergence was likely a result of interaction between the size and ^{15}N abundance of this intervening compartment. Future ^{15}N experiments on plant uptake should include ^{15}N abundance in xylem sap.

Contrary to expectation foliar concentration and contents of N were raised more by AN than urea regardless of the season of application. It had been hypothesized that heavy precipitation in fall would limit efficiency by leaching nitrate from the system. Whereas some nitrate leaching may have occurred the foliar N levels achieved with AN were the highest recorded in the experiment. Two thoughts emerged from this result. First, taken alongside the 18% fertilizer N found in current foliage in the first spring following fall fertilization with urea, there was no reason to suggest that overwinter N acquisition in coastal Douglas-fir is unusual or, even limited relative to "growing season" uptake. Second, despite coarse soil texture and high moisture contents that would optimize movement of ammonium to roots, a nitrate source raised plant availability of N. This suggested that diffusional limitations for NH_4^+ still existed under near optimal conditions presented after fall fertilization. Overwinter uptake of ^{15}N was noted for Douglas-fir by Heilman et al. (1982) but surprisingly little response to this finding has appeared in the literature.

Within urea-fertilized trees maximum ^{15}N enrichment occurred in the first foliar cohort to develop completely after fertilization, irrespective of season of fertilizer application. This turned out to be the 1983 cohort for both seasons of application. A model that explained this observation (Chapter 5, Figure 5-8) was a variation on the proposal of Fagerström and Lohm (1977) that N in tree crowns may be regarded as either mobile or structural. Their model requires that all N for a given new cohort be derived from older foliage whereas our data were better described when a secondary xylem source was included. Because of this two-pool arrangement in foliage, our estimates of 30 to 60% annual turnover in older foliage in the year of fertilization are conservative. In the active pool turnover would be higher.

The continuous cycling of N from older to newer cohorts of foliage resulted in the highest proportion of fertilizer N in current foliage even after 3 growing seasons. Within crowns the allocation of fertilizer N was found to favour foliage in the upper to mid-crown positions where photosynthesis is concentrated.

Cycling of N in trees and soil was described with a kinetically-based simulation model. The availability of fertilizer N to trees in this system was regulated primarily by the mineralization-immobilization cycle. Approximately 135 kg N ha^{-1} was immobilized during the first three weeks after fertilization. Plant N cycling was treated as occurring among structural and mobile pools. Structural N becomes irreversibly bound whereas the mobile pool turns over rapidly and is primarily responsible for the supply of N to growing meristems.

Growth Response of Douglas-fir

Rankings of growth response based on uptake of N alone were accurate for basal area and aboveground biomass increments only. These measures of response relied only on observations of breast height diameter. Basal area growth, which varied between 18 and 59% was in the upper range reported for N-fertilized Douglas-fir. Height growth on the other hand was difficult to rationalize, with greatest increments over control occurring after spring fertilizations, which did not increase foliar N status as much as fall fertilizations.

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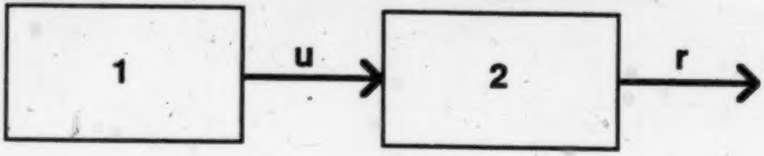
APPENDIX 1. Derivation of equations for foliar N turnover

Consider a two-compartment system with unidirectional flow:



where:

compartment 1 = soil ammonium
compartment 2 = one-year-old foliage
u = N uptake rate
r = N removal rate

We define for compartment i,

X_i = ^{15}N mass
Y_i = N mass

$$A_i = \frac{X_i}{Y_i} = {}^{15}\text{N abundance}$$

We have,

$$\frac{dY_2}{dt} = u - r \qquad [1]$$

$$\frac{dX_2}{dt} = A_1 u - A_2 r \qquad [2]$$

Therefore,

$$\frac{dA_2}{dt} = \frac{d\frac{X_2}{Y_2}}{dt} \qquad [3]$$

and expanding for the derivative of a quotient yields:

$$\frac{dA_2}{dt} = \frac{Y_2\frac{dX_2}{dt} - X_2\frac{dY_2}{dt}}{Y_2^2} \qquad [4]$$

substituting [1] and [2] into [4] yields,

$$\frac{dA_2}{dt} = \frac{Y_2\,(A_1u - A_2r) - X_2\,(u - r)}{Y_2^2} \qquad [5]$$

which simplifies to,

$$\frac{dA_2}{dt} = \frac{u\,(A_1 - A_2)}{Y_2} \qquad [6]$$

Integration of [6] from t_o to t yields:

$$(A_1 - A_2) = (A_1 - A_2)_0\, e^{(u/Y_2)\,t} \qquad [7]$$

Thus uptake may be calculated for any interval from a knowledge of A_2 at initial and final conditions, and provided A_1 and Y_2 are both constant and known. Y_2 may be considered constant but A_1 cannot. A_1 declined exponentially, however (Fig. 5-4):

$$\frac{dA_1}{dt} = - k_1A_1 \qquad [8]$$

where, k_1 = first order rate coefficient

Uptake may then be estimated by substituting,

$$k_2 = \frac{u}{Y_2} \qquad [9]$$

into [6] and solving the resulting equation simultaneously with [8]. The k_2 parameter has dimensions T^{-1}. Uptake may be estimated by multiplying k_2 by Y_2.

APPENDIX 2. Rate constants for processes in soil N model presented in Chapter 6.

Process	LF horizon complex	H horizon & 0-30 cm layer
	--------------wk^{-1}--------------	
Immobilization	0.135	0.4/0.13†
Mineralization from active organic N	0.05	0.025
Mineralization from passive organic N	0.009/0.0007*	0.001
Stabilization	0.025	0.05
Volatilization	0.0075/0*	-
Transfer of NH_4^+ from LF to H to 30 cm layer	0.6/0.055†	-

* Parameter changes at 4 weeks from left to right value

† Parameter changes at 2 weeks from left to right value